

BULLETIN OF THE RESEARCH COUNCIL OF ISRAEL

Section D BOTANY

Bull. Res. Coun. of Israel. D. Bot.

Continuing the activities of the
Palestine Journal of Botany,
Jerusalem and Rehovot Series

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BULLETIN
OF THE RESEARCH COUNCIL
OF ISRAEL

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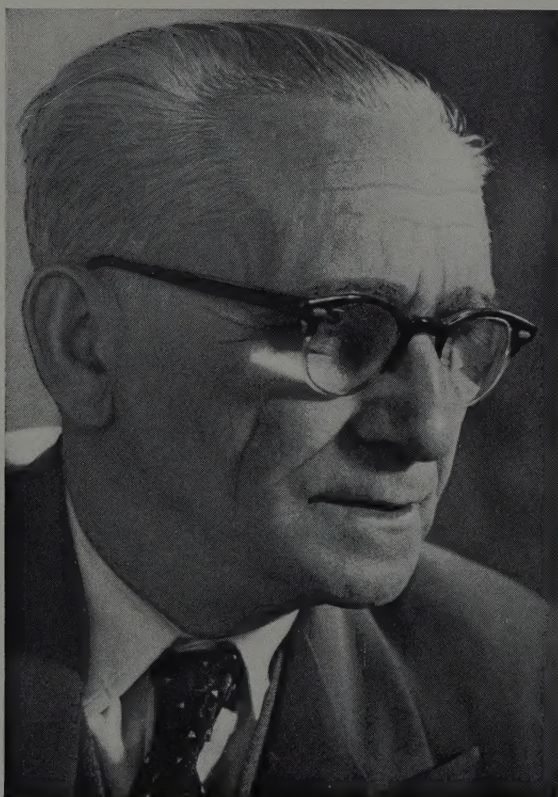
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PROFESSOR MICHAEL ZOHARY

PROFESSOR MICHAEL ZOHARY

In 1920, there arrived in Palestine of that time a young man by the name of Michael Schein later changed to Zohary who was destined to become one of the outstanding botanists of Israel and the Middle East and one of the very few internationally recognized experts of the flora, vegetation and ecology of our region.

Michael Zohary was born in 1898 in Bobrka (Galicia), served as a soldier in the Austrian army during World War I, immigrated to Palestine as a member of the Hashomer Hatsair movement, worked first as a chalutz (pioneer) and in 1922 entered the Hebrew Teachers' Seminary in Jerusalem where he concluded his studies in 1925.

During this time at the seminary, he started on his own to collect plants; he began to identify them and to arrange them in a herbarium. As all this was done on his own initiative and without help, one wonders what instigated young Zohary to start on the way to become a real botanist. The answer is found when one hears Zohary talk to students during an excursion with a plant in his hands and feels that there exists a personal relation between him and the plant. It is this innate love of the plant as a living being which has brought him to Botany.

The herbarium which he started to build up at the seminary, later became a part of the herbarium of the Hebrew University. And here lies the first great merit of Michael Zohary. Together with the late Alexander Eig and Dr. Naomi Feinbrun, he built up through the years the herbarium of the Department of Botany of the Hebrew University which contains today 400,000 sheets of scientifically identified and well mounted specimens of plants of Israel and the Middle East. Without this herbarium, which is quite unique for our region and which was collected with great zeal during the innumerable excursions in Israel and the neighbouring countries, any taxonomic, plant-geographical or plant-sociological work concerning our flora would be quite impossible.

In the summer of 1925, Zohary joined the Department of Botany organized by Alexander Eig at the Agricultural Research Station in Tel Aviv as a part of the Institute for Natural Sciences founded by Professor Otto Warburg. From this time dates the close cooperation and teamwork between Eig, Zohary and Feinbrun which gave us in 1931 the first edition of "The plants of Palestine. An analytical key". This Hebrew book, which today is in its second edition, belongs to the very best of its kind and forms the cornerstone of all botanical studies, as it enables our

scientists, students, farmers and anybody interested in botany to easily identify the plants growing wild in Israel.

In 1928, the department was formally transferred together with its personnel, including Zohary, to The Hebrew University of Jerusalem and moved in 1929 to the premises of the Hebrew University on Mount Scopus in Jerusalem. Whereas up to this time, the main effort of the team was concentrated on the floristic exploration of Palestine, many expeditions to the surrounding countries (Syria, the Syrian desert, Turkey, Iraq, Kurdistan, Transjordan, Sinai, Egypt) during the next ten years widened the scope of Zohary's scientific interests considerably. Based on his outstanding floristic knowledge of the plants growing wild in the Middle East, he became more and more interested in the vegetation in all its many aspects. Phytogeography, ecology, biology *sensu stricto* and phytosociology now became the main themes of Zohary's papers. His Ph. D. thesis which he started in 1931 in Prague and which was published in 1936, is a clear indication of that. In this paper, he investigated the ways and means of many plants of our region to propagate the species through their seeds, fruits and dispersal units. It may be called a classical paper, because Zohary found that contrary to the accepted views many plants of our region possess anti-telechoric devices which instead of enabling the dispersal units to disperse to great distances—limit the dispersal. He paid also attention to the different ways of the dispersal units to germinate and recognized clearly the ecological-biological importance of these phenomena.

After the death of Alexander Eig in 1938, Zohary remained in charge of all the systematic and geobotanical work of the department. Then with the continuously growing number of students, he was able to found his own school of geobotanical research. If we today possess a vegetation map of Israel, a map of the soils in connection with the vegetation, a map of the main plant associations, it is due to Zohary and his geobotanical school. These maps are the result of many years of intense research in the field and have besides their scientific importance great practical importance as well. All this geobotanical work culminated in the publication of two books: *Introduction to the Geobotany of Israel* (1944) and *Geobotany* (1955).

But Zohary, while laying the foundation to a geobotanical understanding of the vegetation of Israel and the Near East, did not forget that without a good floristic knowledge, which is based on the taxonomy of the species, genera and families, no geobotanical work is possible. He therefore started his critical monographic work on difficult genera as for instance *Pistacia*, *Tamarix* and *Quercus*. A Hebrew textbook on systematic botany (*Plant World* 1945) is another witness of his taxonomic interest.

From the beginning of his botanical career, Zohary was convinced that a botanist has an obligation to apply his knowledge to practical problems in addition to his purely scientific work. He has done so successfully in many fields but

especially in the field of afforestation where he helped different public bodies concerned with afforestation to find the most suitable shrubs and trees. His latest Hebrew book written together with A. Fahn, *The Cultivated Plants of Israel* (1957) is another witness of his endeavour to help with his science people working in agriculture and horticulture.

Michael Zohary today at the age of 60 can look back on a full, fruitful and successful life as a botanist. He not only contributed greatly to Botany through his papers and publications, but he succeeded in educating a young generation of botanists (among them his own son) who follow in his footsteps. But Michael Zohary is not the one to look back. He is concerned with the future. We wish him that he may be able to fulfill his dream for the future, to complete together with Dr. Feinbrun his magnum opus, the critical flora of the land of Israel.

MICHAEL EVENARI

XYLEM STRUCTURE AND ANNUAL RHYTHM OF DEVELOPMENT IN TREES AND SHRUBS OF THE DESERT

III. *EUCALYPTUS CAMALDULENSIS* AND *ACACIA CYANOPHYLLA*

A. FAHN

Department of Botany, The Hebrew University of Jerusalem

ABSTRACT

The wood structure, the annual developmental rhythm and the seasonal changes in starch content of *Eucalyptus camaldulensis* Dehnhardt and *Acacia cyanophylla* Lindl. grown in Israel are described.

In *Eucalyptus camaldulensis* development of growth rings commences in (August) September, which corresponds to the spring in Australia, where this species occurs naturally. In the wood the vessels are generally solitary and have spiral thickenings on inner walls as well as vested pits. Vasicentric tracheids and fibre-tracheids occur, but no libriform-tracheids were observed.

In *Acacia cyanophylla* no growth rings were found and the cambium is active throughout the year, reaching a peak during February–May. The vessels are prevailingly arranged in multiples of 2–4 (9), irregular clusters and solitary vessels are also common. The pits are vested.

In both species examined no correlation was found between the changes in starch content of the xylem and the intensity of cambial activity.

The two preceding articles of this series (Fahn 1958 a, b) dealt with the wood structure and annual rhythm of the cambium activity of trees growing within their natural distribution area. It was felt that an investigation of the annual rhythm of xylem production in trees introduced from the southern to the northern hemisphere would be of interest. Such an investigation, therefore, was carried out on *Eucalyptus camaldulensis* Dehnhardt (*E. rostrata* Schlecht.) and *Acacia cyanophylla* Lindl., which are indigenous in Australia and successfully grown in both the Mediterranean and desert parts of Israel.

MATERIAL AND METHODS

Material examined consisted of specimens 3 and 4 of *Eucalyptus camaldulensis* from Masmiya, with trunk diameter of approximately 50 cm and specimens 45 and 46 of *Acacia cyanophylla* from the hills near Jerusalem, with trunk diameter of approximately 20 cm, both localities being situated in the Mediterranean territory of Israel; specimens 6 and 7 of *Eucalyptus*, with trunk diameter of 20 and 25 cm respectively and specimens 20 and 21 of *Acacia cyanophylla*, with trunk

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diameter of approximately 8 cm from sand dunes, 14 kilometres south of Beer-sheba in the desert part of Israel.

Samples of the outermost wood of the trunk were taken for examination at chest height in the case of *Eucalyptus*, and at the height of 50–100 cm in the case of *Acacia*, every month during the period from 2nd November, 1954, to 26th October, 1955, and on several occasions in 1956 and 1957. At the same time, twigs, 4–8 mm in diameter, were also collected.

Methods of preparation and staining of slides were described in the first article of this series (Fahn 1958 a).

EUCALYPTUS CAMALDULENSIS DEHNH.

This species is indigenous to New South Wales, Victoria and South Australia (Bentham 1866).

Wood structure (Figures 1, 3, 5)

Distinct growth rings were observed. The late wood is represented by either one or two narrow bands of tangentially flattened fibres. When two bands are present, between the two a narrow region of wood tissue similar in structure and composition to that of the early wood is found. In cross sections, the vessels are elliptical with their longest axis radially oriented and their maximum tangential diameter being 135 μ . The vessels are predominantly solitary, only occasional multiples of 2–3 being found, which in cross-section of the wood are obliquely arranged. The number of vessels per millimetre varies between (5) 7 and 16 (37). The perforations are simple and mainly transverse, but oblique perforation plates also occur. Vessel members with tailed ends are common. Vessels with spiral thickening on the inner wall were observed. Pits are vested and generally alternate. Tyloses and gummous deposits occur in the vessels. Vessel member length varies from (40) 100 to 400 μ . Vasicentric tracheids are present and vary in length from 350–800 μ . The wood parenchyma is apotracheal-diffuse, and, to a small extent, paratracheal-scanty. The parenchyma stores starch and sometimes contains gummous deposits. The rays are weakly heterogeneous, the outer cells often being of larger vertical and smaller tangential dimensions than the central cells; all cells are procumbent with tangential diameter varying from 12 to 18 μ . The rays are 1–3-seriate and up to 15 cells high, 14–18 rays occurring per millimetre. According to Dadswell and Burnell (1932) the average percentage of biseriate and triseriate rays is 32 and 17 per cent respectively. The ray cells are generally filled with yellow gummous substances. The fibre-tracheids are medium to thick-walled and 0.4–1.0 (1.3) mm long. Pitting is more dense on the tangential wall and the pits are bordered, of the type characteristic of fibre-tracheids (Figure 5). Libriform fibres are absent as already stated by Reinders-Gouwentak (1935).

Rhythm of cambial activity

In the trees examined, the growth-rings, which are easily distinguished microscopically, developed as follows :

Growth-ring development commenced in (August) September. In specimens 3 and 4, growing near Masmiya, development was continuous until mid-May, reaching a maximum in February–April (Table I). In these two trees one or two bands of tangentially flattened fibres were produced between the end of May–beginning of June to the beginning of September. During the period of July–August, the cambial activity was at its lowest, locally even null. New growth rings started to develop at the beginning or middle of September. In trees 6 and 7, growing south of Beersheba, two bands of late-wood could generally be distinguished : the first at the end of March or beginning of April, and the second at the beginning or middle of June. Samples taken on April 15, 1955 exhibited a completed band of flattened fibres and external to it a narrow zone of normal fibres with not fully lignified walls. By 17th June, 1955, the development of the second band of late-wood was in progress. On 22nd August, 1955, the production of the new growth-ring was found to have just commenced in tree 7, while in tree 6 the cambium was still inactive. However, in the sample of 23rd September, 1955, tree 6 already exhibited a few layers of new wood tissue.

Twigs of all specimens examined showed continual cambium activity throughout the year. The period of growth-ring initiation is here apparently variable and not simultaneous in all specimens.

Seasonal changes in starch content

In order to examine the seasonal changes in starch content of the xylem, some sections were treated with I_2KI . On the whole, no positive correlation could be found between the intensity of cambial activity and the width of the starch-free zone. This is contrary to *Tamarix* and *Acacia* spp. (Fahn 1958 a, b), where a broad starch-free zone is always present during the periods of high cambial activity. The *Eucalyptus* specimens exhibited broad starch-free zones during periods of both high and low cambial activity (Table I).

Phenology

Flower buds appeared in July and flowering took place from February to June*. Leaf and shoot development was weak, though continuous, throughout the year, but strikingly intense during May–July in tree 3, June–August in tree 4, and June–July in trees 6 and 7. The growth-ring production and cambial activity of the trunk thus seems not to be correlated with the phenological phases of the trees.



* Flowering has been observed as late as November on trees growing in Rehovot by Prof. H. R. Oppenheimer.

TABLE I
Intensity of cambial activity and seasonal changes in starch content of the xylem in
Eucalyptus camaldulensis

Number of specimen	Type of data	2. Nov. 1954	8. Dec. 1954	5. Jan. 1955	9. Feb. 1955	16. March 1955	15. Apr. 1955	13. May 1955	17. June 1955	18. July 1955	21. Aug. 1955	23. Sept. 1955	26. Oct. 1955
3	A	+4	+5	7-10	20-25	15-20	15-20	+15	1-5	0-2	0-2	+10	+10
	B	5-10	5-10	+20	>200	+40	+60	+40	200-250	>200	>250	+10	20-50
4	A	+10	10-15	—	20-30	+20	30-40	+15	10-15	0-2	+1	1-5	10-15
	B	+40	+20	—	+60	+50	+120	+30	+100	>250	>250	1-5	+70
6	A	15-20	+25	+20	+20	+15	30-40	10-15	2-4	1-2	1-5	3-5	+10
	B	+30	+30	40-50	+60	+60	30-40	15-20	10-15	0-10	0-5	5-10	+40
7	A	+10	+10	+30	+10	10-15	15-20	+10	1-4	0-3	2-10	5-8	10-18
	B	+30	+20	80-100	80-100	60-80	30-40	50-60	+80	0-3	+5	+10	>200

A — number of outermost layers of fibres with incompletely thickened cell walls.

B — width of starch-free zone of outer xylem in number of fibres.

Location of trees: 3 and 4, Masmiya; 6 and 7, 14 km south of Beersheba.

ACACIA CYANOPHYLLA LINDL.

According to Benthams (1864), the natural distribution area of this species is West Australia.

Wood structure (Figures 2, 4)

The wood is diffuse-porous and growth rings are not present. Vessels prevail in multiples of 2-4 (9) and are radially, diagonally and sometimes even tangentially oriented. Irregular clusters and solitary vessels are also common. Maximum tangential diameter of the vessels was found to be 200 μ . Perforations are simple and mostly transverse but diagonal perforation plates also occur, as do vessel members with tailed ends. Vessel member length was found to vary from (60) 100 to 270 μ . Intervascular pitting is generally alternate and pits are vested, medium-sized and with a more or less linear aperture. Tyloses were not observed but gummous deposits do occur. The wood parenchyma stores starch and is paratracheal of the aliform-confluent type. Vertical strands of cells containing rhomboidal crystals are also present. The rays are essentially homogeneous with cell diameters varying from 10 to 33 μ . They are 1-3(4)-seriate, 2-30 cells high and occur 3-6 per millimetre. The ray cells contain yellow gummous deposits but no starch grains were observed. The fibres are moderately thick-walled but groups or solitary gelatinous fibres with very thick walls are scattered amongst them. Fibre pitting is simple and more abundant on the radial walls. Fibre length varies from 0.37 to 1.0 mm.

Rhythm of cambial activity

As mentioned above, no growth-rings could be observed. In trees both growing near Beersheba and Jerusalem, the cambium was found to be active throughout the year, and in all four specimens the maximum cambial activity was observed during February-May (Table II).

Seasonal changes in starch content

Only in tree 45, could a slight correlation be drawn between the width of the starch-free zone in the peripheral xylem and the activity of the cambium. In the three other specimens, no positive correlation was found. As in the case of *Eucalyptus camaldulensis*, a very broad starch-free zone appeared, contrary to expectation, during periods of relatively low cambial activity (Table II).

Phenology

Inflorescences appeared in January. Slight leaf development was observed throughout the year with a sudden outburst of leaf and shoot development during March-May (June). This period of increased development coincides with that of maximal cambial activity in the trunk.

TABLE II
Intensity of cambial activity and seasonal changes in starch content of the xylem in
Acacia cyanophylla

Number of specimen	Type of data	2. Nov. 1954	8. Dec. 1954	5. Jan. 1955	9. Feb. 1955	16. March 1955	15. Apr. 1955	13. May 1955	17. June 1955	18. July 1955	21. Aug. 1955	23. Sept. 1955	26. Oct. 1955
20	A	1-3	+8	+5	15-20	15-20	—	5-10	+5	1-4	1-4	0-1	1-3
	B	1-3	+8	+5	40-60	+60	—	>200	>400	1-5	2-10	5-10	>20
21	A	2-5	1-3	2-4	+15	7-10	7-10	7-10	5-8	5-10	+5	2-3	0-2
	B	2-5	2-5	2-5	+30	7-10	7-10	+10	+15	>400	5-10	3-5	0-2
45	A	5-10	10-15	10-15	20-25	30-40	+30	+30	+10	+10	+10	+10	+10
	B	10-15	+25	+15	20-25	60-80	30-40	+40	+30	+10	+10	10-15	+20
46	A	3-5	7-10	+10	+20	3-40	+30	+20	+10	4-8	3-8	4-6	3-4
	B		+10	+10	+20	60-70	+60	50-70		+30	>250	+10	>300

A — number of outermost layers of fibres with incompletely thickened cell walls.

B — width of starch-free zone of outer xylem in number of fibres.

Location of trees: 20 and 21, 14 km south of Beersheba; 45 and 46, near Jerusalem.

DISCUSSION

Reinders-Gouwentak (1935) states that growth rings are generally absent in *Eucalyptus camaldulensis*. Greiss (1939) found growth-rings to be present in both irrigated and non-irrigated trees grown in Egypt. All trees examined by the present author produced distinct growth-rings and so the course of their seasonal development could be followed. The most salient point emerging from this investigation is, that in Israel growth-ring production in the trunk commences in late summer (August–September) before the winter rains. The maximal production of xylem cells, was found to occur during February–April in the Mediterranean part and about a month earlier in the desert part of Israel. Amos et al. (1950) found the growth-ring formation in *Eucalyptus gigantea* Hook. f., growing in South Australia, to begin in the same month (September), i.e. in the spring of the southern hemisphere. Near Masmiya, in the Mediterranean territory, late-wood was produced in May, which coincides with the time of late wood production in *Eucalyptus gigantea* (Amos et al., 1950). In the desert part of Israel, south of Beersheba, two proximate and sometimes confluent bands of late wood were produced, one at the end of March or beginning of April and the other by the beginning or middle of June. In all specimens of *Eucalyptus* the period of minimal or null activity is short, approximately simultaneous with that of *Eucalyptus gigantea* in South Australia. The synchronization of growth-ring development in trunks of *Eucalyptus* trees growing in their natural habitat in the southern hemisphere, and in others of the same species at a similar latitude in the northern hemisphere, does not seem to be explicable without the assumption of an endogenic rhythm, the existence of which in other cases of growth-ring development was already suggested by Bünning (1948). Thus generally trees of *Eucalyptus camaldulensis* seem to preserve the annual rhythm of growth ring production in accordance with the seasons prevailing in their original habitat, even after several generations of growing in a different climatic rhythm. The intensity of wood production, however, appears to be influenced by the climatic conditions of the new habitat.

No data on *Acacia cyanophylla* from Australia were found for comparison.

In the specimens examined, the wood-structure differs from that of *A. tortilis* and *A. raddiana* (Fahn 1958 a and b) especially by the much smaller number of gelatinous fibres and by the presence of yellow gummous deposits in the ray cells. In *A. cyanophylla*, no annual growth-rings could be distinguished and the cambium was active throughout the year, even in trees growing near Jerusalem where winter temperatures are low. Maximal cambial activity was found in February–May, both near Jerusalem and south of Beersheba.

In contrast to the species of *Tamarix* and *Acacia* described in previous papers (Fahn 1958 a and b), no positive correlation could be found in *Eucalyptus camaldulensis* and *Acacia cyanophylla* between the changes of starch content of the xylem and the intensity of cambial activity.

A similar lack of correlation was found by Wight (1933) for *Pinus sylvestris* L. Wight, therefore, expressed the view that cambial activity and changes in starch content are two distinct seasonal cycles — "a growth cycle of activity and dormancy and a physiological adjustment to the starch-sugar equilibrium".

Observations on other plant species, e.g. *Vitis vinifera* L. (Esau 1948, Bernstein and Fahn 1959) and *Tamarix* spp. (Fahn 1958a) revealed a correlation between the two cycles. It seems thus that although these cycles are distinct, cambial activity influences the starch content. This influence, however, may sometimes be relatively slight or even suppressed by other physiological factors.

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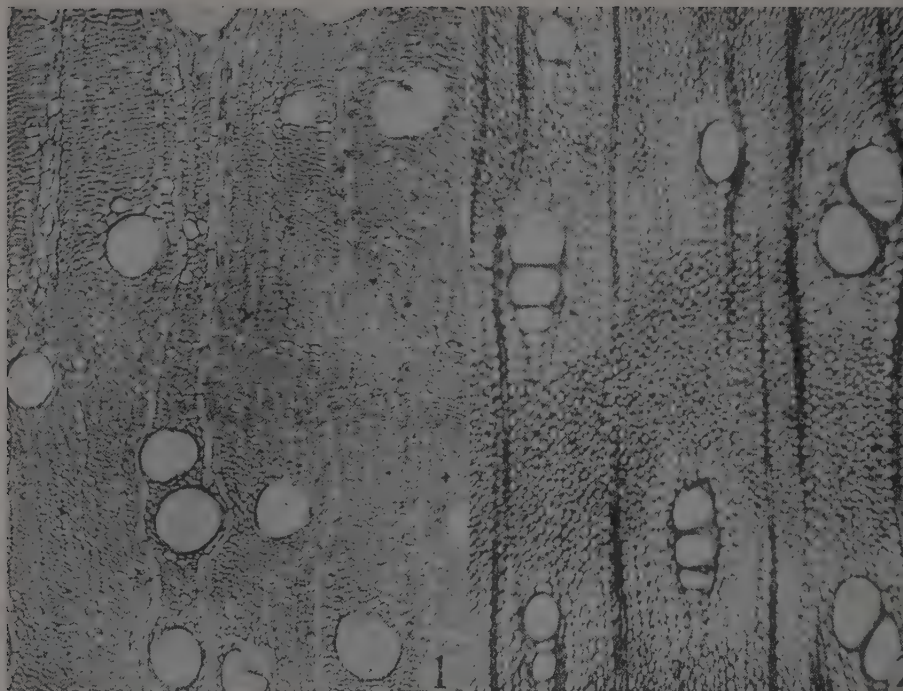


Figure 1. *Eucalyptus camaldulensis*, cross-section of wood. $\times 80$. Figure 2. *Acacia cyanophylla*, cross-section of wood $\times 80$. Figure 3. *Eucalyptus camaldulensis*, tangential section of wood. $\times 190$. Figure 4. *Acacia cyanophylla*, tangential section of wood. $\times 150$.

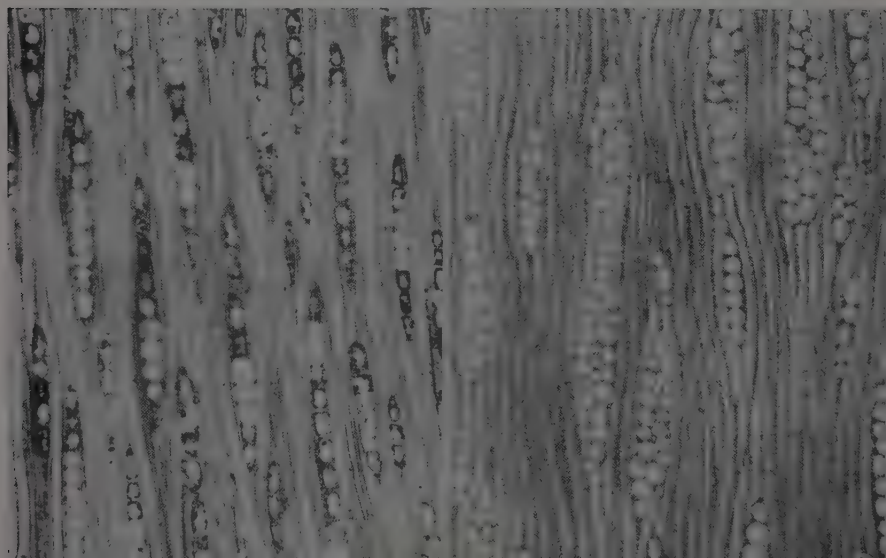




Figure 5. *Eucalyptus camaldulensis*, tangential section of wood, showing fibre-tracheids the bordered
nit pores of which exhibit bordered cells.

SPONTANEOUS *PINETA* IN THE LEBANON

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ABSTRACT

During the summers of 1941 and 1942 *Pinetum pineae* and *Pinetum brutiae* were studied by the author in Southern and Central Lebanon.

The analysis of the phytosociological records is given in Tables III, IV and V.

The relationships of three *Pineta* of the Lebanon, *Pinetum pineae*, *Pinetum brutiae* and *Pinetum halepensis*, with the main Mediterranean vegetation units are discussed. These *Pineta* form part of the sclerophyllous forest belt of Markgraf (1932) and belong to the order *Quercetalia calliprini*, class *Quercetea calliprini*.

The author supports the viewpoint that the *Pineta* are to be regarded as climax associations. These climax associations are found in areas governed by specific edaphic conditions, and are surrounded by more extensive areas of the *Quercetum calliprini* climax.

The indigeneity of the *Pinetum pineae* forests in the Lebanon is discussed. The alleged introduction of *Pinus pinea* into Lebanon by Fakhr-ed-din in the 17th century is shown to be legendary.

The data collected by the author are in agreement with the view that *Pinetum pineae* in the Lebanon is a natural type of vegetation. The opinion expressed is substantiated by:

- (a) the floristic composition of the forest,
- (b) the close correlation found between the location of *Pinetum pineae* forests and that of the Lower Cretaceous sandstone.

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The spontaneity of *Pinus pinea* forests in the Lebanon

INTRODUCTION

Literature on the vegetation of the Lebanon is surprisingly scarce (Kotschy 1864, Post 1889, Mouterde 1947, Pignatti 1952, Delbes 1955). Some data on ecological conditions of the main vegetation types can be found in geological papers on the Lebanon (Fraas 1876, Diener 1886, Dubertret 1949-51).

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The present study is based on notes and phytosociological records taken during two brief visits to Southern and Central Lebanon in the summers of 1941 and 1942. At an earlier date (1934) the author had participated in a research trip to the Northern Lebanon headed by the late A. Eig. The results of that visit were unfortunately never published.

The author's itinerary in the Southern and Central Lebanon is shown on Maps 1, 2. In short it ran as follows:

1941: Beirut — Hammana; Hammana — El Barouk; Hammana — Douhour Choueir — Beirut.

1942: Saida — Djezzine — Hammana — Douhour Choueir — Beirut. The study was concerned chiefly with *Pinetum pineae*.

PHYSIOGRAPHIC DATA

Orographically, the country is dominated by a mountain block extending in a south-south-westerly to north-north-easterly direction. The coastal plain is very narrow, except in a few places. The mountains are fairly steep in the west, rising up to 2000 m at Jebel Barouk, 2550 m at Jebel Sanin and 3088 m at Qornet es Saouda. In the East, they drop steeply into the Bequa'a (600 m above sea level) which is the prolongation of the Great Rift Valley. The greater part of the region studied lies at altitudes of 900–1200 m.

The climate is characterized by a dry season lasting from May to October. Annual rainfall ranges from 600 mm on the coast to 1500 mm at higher altitudes (Dubertret, Ashbel). In the mountains snow falls every year, yet at heights of 900–1200 m periods of low temperatures are short.

For an understanding of the distribution of the main vegetation types some knowledge of the country's geological features is essential. It is, therefore, fortunate that during the last ten years new geological maps on a scale of 1:50,000 have been published by Dubertret and his collaborators (1949–1951). Relevant to the present paper are the Saida, Djezzine and Beirut map sheets.

The Lebanon is built mainly of sedimentary rocks ranging from the Jurassic to the Quaternary. It originated as a part of the Syrian Plateau, but has been greatly affected by subsequent tectonic movements. Their results are: (1) the main rift of Yammounh in the East, (2) a long flexure running almost parallel to the coast on the West, and (3) a series of more or less transversal rifts crossing the country. These facts of tectonic past cause a discordance of strata which is frequently revealed on the surface. In addition, deep valleys often present natural profiles of successive strata.

As a rule, changes in geological substratum are clearly reflected in changes of vegetation.

The main geological strata of the Lebanon and their lithological features are presented in Table I.

TABLE I
Chronology and lithological features of strata in the Lebanon

Age		Symbol on the map of Dubertret	Lithological features
Jurassic		j ₆ j ₇	Mostly compact limestones; some marly limestones and a volcanic level of basalt, cinerites and various sediments.
Lower Cretaceous	Basic sandstone	C ₁	Sandstone built of granit quartz cemented by ferrum oxides; varies in stratification and in hue, ranging from violet and red to rose and white.
	Lower Aptian	C _{2A}	Thin strata of quartz sandstones, sandy clay and marls intercalated with various calcareous limestones.
	Upper Aptian	C _{2B}	Apart from similar strata contains a prominent feature known as Blanche's wall — a compact limestone bank which is about 50 m thick.
Middle Cretaceous	Albian	C ₃	Bank of limestone alternating with a green marl; absence of quartz.
	Cenomanian-Turonian	C ₄	Banks of limestone intercalated with thin layers of marly chalks.
Upper Cretaceous	Senonian	C ₅	White marls and marly chalks.
Tertiary	Eocene	e	Marly chalks with layers of black flint.
	Miocene	m	
	Pliocene	p	

The Jurassic limestones build the ridge of Djebel Niha and Djebel Barouk (map of Djezzine), as well as a great portion of the northern half of the Beirut map. In addition, the Jurassic formation appears in narrow strips in the ravine of Wadi Damour and near the Roûm village.

Cenomanian formations — dolomites, limestones and marls — occupy large parts of the Saïda and Djezzine map sheets.

The Lower Cretaceous sandstone, "grès de base", appears in patches and outcroppings in the Djezzine, as well as in the southern half of the Beirut sheets. *Pinus pinea* forests are confined to that sandstone.

VEGETATION BELTS AND CLIMAX COMMUNITIES IN THE LEBANON

Margraf (1932) and Regel (1944) described Mediterranean vegetation belts, with ecological-physiognomic features as basis. Three of these vegetation belts are represented in the Lebanon: a) the sclerophyllous forest belt, b) the summer-green forest belt and c) the Mediterranean needle-forest belt. The upper edge of the needle-forest belt forms the timberline and borders on the tragacanth vegetation

of the highest elevations of the Lebanon. In some places, the Mediterranean needle-forest appears in direct contact with the sclerophyllous forest. Table II shows the altitudinal ranges of each of the three belts in the Lebanon. The forest communities discussed in the present paper belong to the sclerophyllous forest.

TABLE II
Altitudinal ranges of vegetation belts in the Lebanon

Sclerophyllous forest belt	up to 1300—1400 m
Summer-green forest belt	1300—1800 m
Mediterranean needle-forest belt	1500—2300 m

Regel (1944) pointed out that the climax communities of the sclerophyllous forest belt, known from the Western Mediterranean and described by Lüdi (1935) under the *Quercion ilicis* climax belt from Italy and by Schmid (1936) and Frei (1938) under the *Quercus ilex* belt, are replaced in the Eastern Mediterranean by the communities of *Quercion cocciferae*. In the following we refer to these communities as belonging to *Quercetalia calliprini*.

The arboreal climax communities of the *Quercetalia calliprini* sclerophyllous forest belt are:

Ceratonia siliqua — *Pistacia lentiscus* association

Quercion calliprini associations

Pinion halepensis associations

Pinion brutiae associations

Pinion pineae associations.

The communities of the summer-green forest belt are *Quercetum cerridis* and allied associations; those of the Mediterranean needle-forest: *Cedretum libani*, *Abietum cilicicae*, *Juniperetum excelsae* and allied associations.

The forests of *Pinus nigra* ssp. *pallasiana* which appear above the *Pinus brutia* forests in Asia Minor, Amanus and Cyprus, do not occur in the Lebanon.

A difference of opinion exists as to whether the pine forests of the sclerophyllous forest belt in the Mediterranean are to be regarded as climax communities. Walter (1956) and others do not consider the pine forests as climax communities, but as transition stages which tend to develop into a climax of *Querceta*.

The present author does not share this view. Observations made in Palestine, the Lebanon and Cyprus, as well as data from literature on *Pineta* in Italy, Greece and Asia Minor seem all to lead to one conclusion: with only a few possible exceptions, the various *Pineta* (*Pinetum halepensis*, *Pinetum brutiae*, *Pinetum pineae*) are confined to specific edaphic conditions under which *Querceta* do not occur as a rule.

In the East-Mediterranean climate the rocks underlying *Pinetum halepensis* and *Pinetum pineae* do not give rise to developed soil horizons, but disintegrate into a crude soil. The edaphic conditions of such sites are unsuited to associations of *Quercion calliprini*. Thus *Quercetum calliprini* has no chance of developing successfully on the site of a *Pinetum halepensis*, even when given time. Though within various *Pineta* shrubs of *Quercus calliprinos* are usually found, they are as a rule less well developed than when growing within a *Quercetum calliprini*.

For the Western Mediterranean Schmid (1949) describes a similar relationship between associations of *Quercion ilicis* and various *Pineta*. All types of *Pineta* within the *Quercus ilex* belt are confined to specific soil conditions, and their habitats are relatively restricted in area. These habitats are surrounded by the regional biocoenoses of the *Quercus ilex* forest. The local biocoenoses formed by *Pinus* species occupy "nutritionally poorer sandy soils or nitrogen-poor rocky calcareous soils" (Schmid, p. 187).

In our part of the Mediterranean, it is impossible to state with certainty which of the edaphical requirements of *Quercetum* remain unfulfilled on the substratum bearing a *Pinetum*, be it water relations, mineral or organic soil compounds or other factors. At any rate, it seems that the *Pinetum* itself does not change these factors in a direction favourable for *Quercetum* development.

The inference from all these considerations is that *Pineta* are to be regarded as climax communities.

PHYTOSOCIOLOGICAL DATA

This study concentrates on three types of *Pineta*, i.e. *Pinetum pineae*, *Pinetum brutiae* and *Pinetum halepensis* of which phytosociological records by the method of Braun-Blanquet were taken during the visits to the Lebanon. All records reflect the autumn aspect of the forests and, with very few exceptions, contain no annual or perennial herbs. 19 sample records were taken in *Pinetum pineae*, 6 in its sub-association *brutietosum*, 3 in *Pinetum brutiae*, and one in *Pinetum halepensis*. Analytical tables were compiled for the two former associations. The discussion of *Pinetum halepensis* is based on the author's extensive material of records collected throughout Palestine.

The following phytosociological classification is accepted:

Class *Quercetea calliprini* (Zohary 1955)

Order *Quercetalia calliprini* (Zohary 1955)

Alliance *Pinion pineae*

Association *Pinetum pineae libanoticum*

Subassoc. *Pinetum pineae brutietosum*

Alliance *Pinion brutiae*

Association *Pinetum brutiae libanoticum*

Alliance *Pinion halepensis*

Association *Pinetum halepensis*

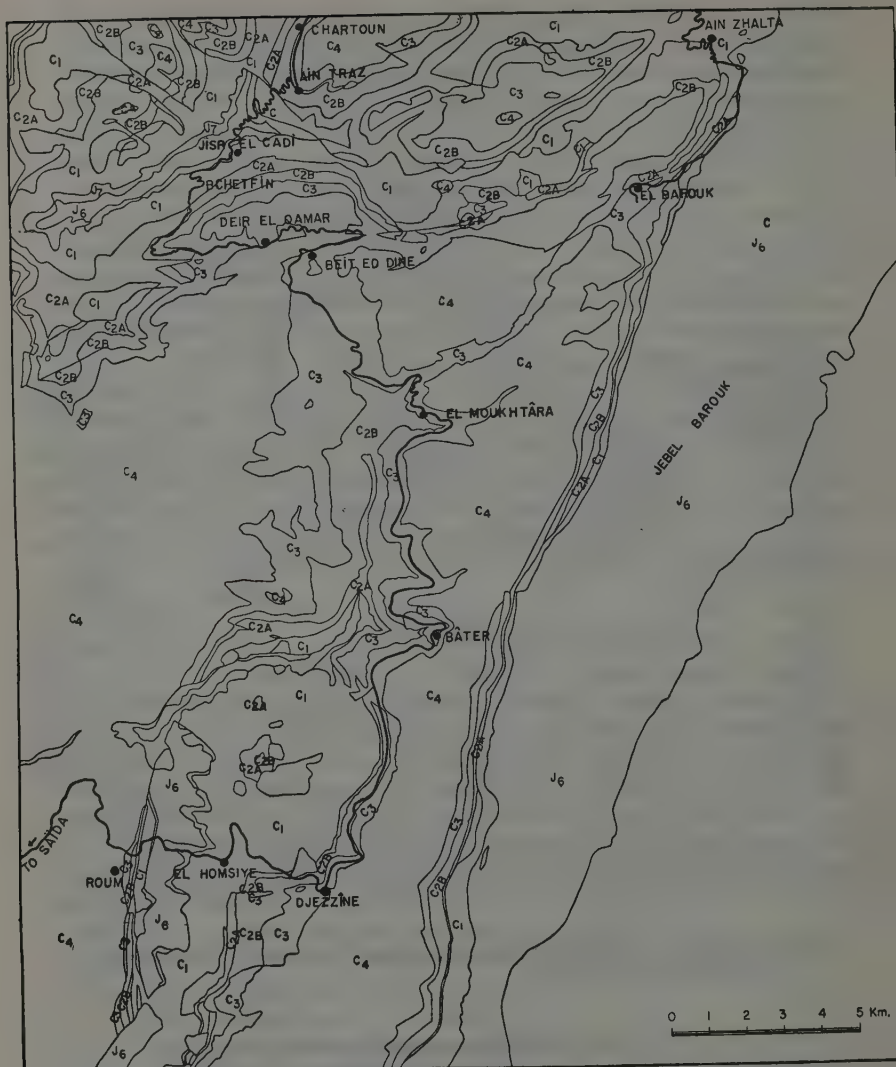


Map 1. Geological map of the Beirut area adapted from L. Dubertret (1945) showing the itinerary of the author.

LEGEND

Heavy line showing the route of the author

- | | | | |
|----------|------------------------------|----|-----------------------|
| J6, J7 | — Jurassic | C3 | — Albian |
| C1 | — Lower Cretaceous sandstone | C4 | — Cenomanian—Turonian |
| C2A, C2B | — Lower and Upper Aptian | C6 | — Senonian |



Map 2. Geological map of the Djezzine area adapted from F. Heybrock and L. Dubertret (1945) showing the itinerary of the author.

LEGEND

Heavy line showing the route of the author

j₆, j₇ — Jurassic

C₁ — Lower Cretaceous sandstone

C_{2A}, C_{2B} — Lower and Upper Aptian

C₃ — Albian

C₄ — Cenomanian—Turonian

C₅ — Senonian.

In the Western Mediterranean, *Pinetum pineae* and *Pinetum halepensis* are included in the order *Quercetalia ilicis* and class *Quercetea ilicis* (Braun-Blanquet et al. 1952, Francini 1953).

Pinetum pineae libanoticum

In the Lebanon *Pinetum pineae* is confined to the Lower Cretaceous sandstone. Accordingly, this forest type is found chiefly in Southern and Central Lebanon where that sandstone occupies larger areas. *Pinetum pineae* occurs there on every possible exposure as well as on flat ground.

It is a forest of spaced trees, and its general coverage rarely reaches 100%. The underwood consists mostly of shrubby *Quercus calliprinos* and *Juniperus oxycedrus*. Where the forest is more open, *Cistus villosus* and *Cistus salvifolius* account for a large part of the coverage. *Lavandula stoechas* is very prominent.

The differences in floristic composition in the recorded *Pinetum pineae* stands result most probably from ecological conditions in various sandstone layers. The layers display variation in colour and firmness, as well as in thickness and in the mode of weathering. The most common sandstone variety in *Pinetum pineae* is a ferruginous red sandstone. Violet, grey, yellow and whitish sandstone strata are also fairly common. The rock is either composed of thin layers varying in hue, or disintegrates into large firm blocks which show no stratification. Sometimes the surface layer of a dark-coloured firm sandstone disintegrates into polygonal pieces 2-3 cm in diameter. Farmers expressed the opinion that the yellowish-red sandstone producing a sandy soil contains more water and is more favourable for *Pinea* forests, than the violet variety forming polygonal gravel.

Sometimes the sandstone strata are intercalated with impervious layers, resulting in the formation of small springs. Hydrophytic plants are found in such habitats. At a small spring near Douhour Choueir (Central Lebanon) *Drosera rotundifolia* was found by the author together with a few ferns, such as *Osmunda regalis*, *Blechnum spicant* and several marsh species (Feinbrun 1942). The occurrence of *Rhododendron ponticum* and *Erica verticillata* in some of the records is also the result of some specific combination of edaphic conditions. The proximity of water-bearing strata is often reflected in the better development of some associates which require higher moisture content in the soil, such as *Quercus infectoria* (record no. 9). A combination of drier strata, on the other hand, results in a poor floristic composition of the forest. Apparently the red type of sandstone gives the nearest approximation of a "normal" composition of *Pinetum pineae* in the Lebanon.

The soil pH in the habitat of *Drosera rotundifolia* was examined and found to be 6.4-6.9 (Feinbrun 1942). These values approach those found in *Pinetum pineae* and *Pinetum brutiae* in W. and SW. Anatolia (Schwarz 1936).

The floristic composition of *Pinetum pineae* in the Lebanon can be seen from Table III. This Table is based on 19 phytosociological records, 9 of which are

TABLE III

Analytical table of association *Pinetum piniae libanoticum*

Number of record	Altitude in metres	Slope exposure	Approximate age of <i>Pinus pinia</i> in years	Height of <i>P. pinia</i> in metres	General coverage	Surface in m ²	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
							1200	1000	1000	900	1200	1200	ca900	ca900	ca900	450	450	350	700	900	800	1200	1000	950	900	
							slight	SE	—	—	SW 40°	W 40°	N 15°	—	—	70°	N 40°	—	—	—	—	—	—	—	E	
							8-10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	90%	
							100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	
CHARACTERISTICS OF ASSOCIATION																										
<i>Pinus pinia</i>	3	3	(+)*	(+)																						
<i>Rhododendron ponticum</i>																										
<i>Erica verticillata</i>		+																								
<i>Helianthus umbellatum</i> var. <i>syriacus</i>																										
<i>Origanum ehrenbergii</i>																										
<i>Wiegandieria daschampsii</i>		2																								
<i>Phleum montanum</i>																										
DIFFERENTIAL COMPANION																										
<i>Levandula stoechas</i>	1	3		(+)																						
CHARACTERISTICS OF ORDER QUERCETALIA CALLI- PINI ESPECIALLY FREQUENT IN PINETA																										
<i>Juniperus oxycedrus</i>	+	1																								
<i>Cupressus sempervirens</i>	2	+	(+)	(+)																						
<i>Cistus villosus</i>																										
<i>Cistus salviifolius</i>																										
CHARACTERISTICS OF ORDER QUERCETALIA CALLI- PINI AND OF CLASS QUERCETIA CALLIPRINI																										
<i>Quercus ilex</i>	+			(+)																						
<i>Quercus calliprinos</i>	+																									
<i>Pistacia palaestina</i>																										
<i>Arbutus andrachne</i>																										
<i>Sisyrinchia officinalis</i>																										
<i>Rhamnus palaestina</i>	1			(+)																						
<i>Calycotome villosa</i>	1-2	+		(+)																						
<i>Poterium spinosum</i>	3	+		(+)																						
<i>Dactylis glomerata</i>																										
<i>Scabiosa ucrania</i>																										
<i>Stipa bromoides</i>																										
ACCIDENTALS																										
<i>Myrtus communis</i>																										
<i>Ostrya alba</i>	+																									
<i>Quercus libani</i>																										
<i>Sorbus</i> sp.																										
<i>Crataegus monogyna</i>																										
<i>Genista sphacelata</i>																										
<i>Pteris aquilina</i>																										
<i>Teucrium divaricatum</i>																										
<i>Microseris juliana</i>	+																									
<i>Poa bulbosa</i>																										
<i>Briza maxima</i>																										

* (+) = Presence without phytosociological evaluation

incomplete in that they lack the abundance — dominance values. Degrees of sociability are not recorded in the Table. Records nos. 1–6 were taken in Central Lebanon on 15–18.9.1941, nos. 7–12 in Southern Lebanon on 19–22.9.42 and nos. 13–19 on 22–24.9.42.

The following are details of the records:

Rec. no. 1. Falourha, 1 km north of Hammana. Red sandstone. *Quercus calliprinos* as a small tree, approx. 3 m high.

Rec. no. 2. Ain Zahalta, near the hotel. Reddish sandstone. *Pinus pinea* as a tall tree; *Juniperus oxycedrus* 25–40 cm high.

Rec. no. 3. Nabaa es Safa, approx. 10 km southwest of Hammana. Sandstone near water course.

Rec. no. 4. Area between Qornâyel and Bzebdine, north of Hammana. Red sandstone.

Rec. no. 5. Douhour Choueir. Sandstone.

Rec. no. 6. as in Rec. no. 5; western slope facing the sea.

Rec. no. 7. Area west of Djezzine, near the road to Homsiyé, 900 m. Red sandstone. *P. pinea* trees of various ages growing 3–4 m apart (15 m high and 30 cm thick; 3–4 m high and 8 cm thick respectively). Stunted *Qu. calliprinos* and *Qu. infectoria*.

Rec. no. 8. Several hundred metres from Rec. no. 7. *P. pinea* trees of various ages, including seedlings.

Rec. no. 9. Small wadi on sandstone near the site of record no. 8. *Qu. infectoria* forming tall trees, *Qu. calliprinos* shrubby.

Rec. no. 10. Bshetfine to Jisr el Cadi. Rocky sandstone on steep slope. *Cupressus sempervirens* as 1–8 m high trees.

Rec. no. 11. Near the site of record no. 10, not far from a stand of *Pinetum pineae brutietosum*.

Rec. no. 12. Blata, S. of Chartoûn. Trunks of *P. pinea* 15–20 cm thick, with 1–2 year old seedlings also occurring. Dwarf *Qu. infectoria*.

Rec. no. 13. Qafr Oumai, betw. Jisr el Cadi and Bhamdoûn. Sandstone. Trunks of *P. pinea* 15 cm thick; also seedlings.

Rec. no. 14. Qoubbé, 4 km W. of Hammana. Sandstone. *P. pinea* trunks 12–15 cm thick; 1 year old seedlings also found. Small shrubs of *Qu. infectoria* and *Juniperus oxycedrus*.

Rec. no. 15. Bmariam, 2 km west of Hammana. Sandstone. Very old specimens of *P. pinea*; among them trees 500 years old, with a circumference of 3.5 m, trees 200 years old with trunks 60–70 cm in diameter and trees 120 years old reaching 20 m in height.

Rec. no. 16. N. of Hammana, near Qornâyel. Sandstone.

Rec. no. 17. Qornâyel to Salîma. Yellowish-red sandstone forming a yellow sandy soil. *P. pinea* trees about 4–7 m apart.

Rec. no. 18. Below Rec. 17. Small wadi. Reddish sandy soil.

Rec. no. 19. Qornâyel to Bzebdine. White and brownish sandstone. Specimens of *Qu. calliprinos* few and small.

Stands of *P. pinea* were also observed in several other localities.

Pinetum pineae brutietosum

Records nos. 20–23, were taken near Roûm in Southern Lebanon on 20–21.9.42 and records nos. 24–25 between Deir Qamar and Bshetfine (Table IV).

Records nos. 20–23 were taken in a contact area between narrow strips of Jurassic and Aptian limestones and of the Lower Cretaceous sandstone ("grès de

TABLE IV
Analytical table of subassociation *Pinetum pineae brutietosum*

Number of record	20	21	22	23	24	25	Presence
Altitude in metres	900	900	1000	940	700	450	
Slope and exposure	—	W30°	W	E10°	N30°	N	
General coverage	—	60%	—	80-90%	—	100%	
Surface in m ²	100	100	100	100	100	100	
DIFFERENTIAL CHARACTERISTIC OF SUBASSOCIATION							
<i>Pinus brutia</i>	(+)* (1-2 m)	2	(+)	2 (dwarf)	2-3 (8-10 m)	1	6
CHARACTERISTICS OF ASSOCIATION							
<i>Pinus pinea</i>	(+)	3	(+)	2	1	+	1
<i>Halimium umbellatum</i>	+						6
DIFFERENTIAL COMPANION							
<i>Lavandula stoechas</i>	(+)	2	(+)	3	3	2	6
CHARACTERISTICS OF ORDER QUERCETALIA CALLIPRINI ESPECIALLY FREQUENT IN PINETA							
<i>Juniperus oxycedrus</i>	(+)	3	(+)	2			4
<i>Cupressus sempervirens</i>						2	1
<i>Cistus salvifolius</i>	(+)	3	(+)	3	2	3	6
<i>Cistus villosus</i>			(+)	2	2	1	4
<i>Phleum montanum</i>		+					1
CHARACTERISTICS OF ORDER QUERCETALIA CALLIPRINI AND OF CLASS QUERCETEA CALLIPRINI							
<i>Quercus infectoria</i>	(+) (2-3 m)	+	(+)	+	1-2	1	6
<i>Quercus calliprinos</i>	(+) (20 cm)			+	2	2	4
<i>Arbutus andrachne</i>						+	1
<i>Styrax officinalis</i>				+			1
<i>Rhamnus palaestina</i>					1		1
<i>Acer syriaca</i>					+		1
<i>Crataegus azarolus</i>			(+) (small)				1
<i>Spartium junceum</i>					1		1
<i>Salvia triloba</i>					1		1
<i>Calycotome villosa</i>	(+)	1	(+)	1	2-3	1-2	6
<i>Dactylis glomerata</i>					1		1
<i>Stipa bromoides</i>			(+)		2	1	3
<i>Helichrysum sanguineum</i>					2		1
ACCIDENTALS							
<i>Myrtus communis</i>	(+)					1	2
<i>Teucrium divaricatum</i>					3		1
<i>Poa bulbosa</i>		+				1	2
<i>Briza maxima</i>		+			+		2
<i>Atractylis comosa</i>		+					1

* (+) = Presence without phytosociological evaluation.

base") east of Roûm. In this rift area the soil produced from both sandstone and limestone enables *Pinus brutia* to enter into *Pinetum pineae*. A similar situation was found in the valley of W. Damour (Rec. nos. 24–25) where on the slope of a deep ravine the sandy soil derived from sandstone mixed with calcareous soil from under- and overlying limestones.

Details of the sites of records nos. 20–25 follow.

Rec. no. 20. Between Roûm and Homsiyé. Sandstone. *Pinus brutia* trees are only 1–2 m high, i.e. much lower than in the adjoining *Pinetum brutiae* (rec. no. 28).

Rec. no. 21. About 150 m east of Rec. 20. *P. pinea* trees 10–15 m high, trunks 10–40 cm in diam. *P. brutia* much smaller (1–2 m; with only a few specimens up to 5 m high).

Rec. no. 22. Homsiyé. Sandstone. *P. brutia* forming small trees.

Rec. no. 23. East of Homsiyé. Sandstone. Very small *P. brutia* trees.

Rec. no. 24. Descent to Wadi Damour. A sandstone block at the foot of a dolomite slope. Mixed calcareous and sandstone boulders; soil containing sand and chalky gravel. *P. brutia* trees 8 m high.

Rec. no. 25. North of Bshetfine. Sandy soil.

P. brutia trees in this subassociation are often fairly well grown, but on the whole do not reach the development of the trees found in *Pinetum brutiae* stands. It is apparent that in the Lebanon the Lower Cretaceous sandstone does not meet the optimal requirements of *P. brutia*.

Schwarz (1936) describes a similar type of *Pinetum pineae* in western Anatolia and notes that soil conditions are transitional between those prevailing in *Pinetum pineae* and in *Pinetum brutiae* proper. In Western Anatolia as against Lebanon the *Pinetum pineae* is far more restricted than the *Pinetum brutiae*. Schwarz writes: "In Kozak *Pinus pinea* roots almost exclusively on granite; its forests are embedded in, and enclosed by the Brutia-pine forest that occupies a different kind of soil" (p. 362).

The floristic composition of subassociation *brutietosum* (Table IV) does not differ from that of the main type, and its differential characteristic is *P. brutia*.

Schwarz's opinion that *Pinetum pineae* is only a variation of *Pinetum brutiae* (p. 364) does not seem justified. *Pinetum pineae* in the Lebanon is characterized by a number of species with a preference to, or exclusive appearance on sandstone derived sandy soil. These are *Halimium umbellatum* var. *syriacum*, *Origanum ehrenbergii*, *Weingartneria deschampsoides*, *Lavandula stoechas*. It is also significant for the ecological conditions prevailing in *Pinetum pineae* that no climbers are found there, and the number of tree and shrub species characteristic of the order *Quercetalia calliprini* is much smaller than in *Pinetum brutiae*.

Many of the records of *Pinetum brutiae* cited by Schwarz comprise *P. pinea*, and it seems that they represent the subassociation *brutietosum* of *Pinetum pineae*.

Pinetum brutiae libanoticum

The records of *Pinetum brutiae* were taken in Southern Lebanon west of Djezzine (20 Sept. 42). The area occupied by this forest type appears on two adjoining narrow strips designated on Dubertret's map as Jurassic and Aptian formations (j_6 , c_2).

The details are as follows:

Rec. no. 26. East of Roûm. Very rocky ground of Aptian (?) grey rock with terra-rossa collecting among the projecting boulders. Soil covered with needles.

Rec. no. 27. Near Rec. no. 26. Terra-rossa covered with needles.

Rec. no. 28. About $\frac{1}{2}$ km eastward in the direction of Djezzine.

Pinetum brutiae has been observed by the author also in Northern Lebanon (map Sir ed Danié of Dubertret) near Tormaz on Jebel Termalikh, ca 700 m, on a white soft chalk and near Jebel Qamua 1400 m, both on Cenomanian formation (c_4 by Dubertret). Unfortunately records made there by the late A. Eig are not available for comparison.

The floristic composition of records nos. 26–28 and an analysis of the association are given on Table V. Since the number of records as well as the area investigated are restricted, the analytical table is fairly incomplete. So far *P. brutia* seems to be the sole characteristic representative of the association.

P. brutia, the main component of *Pinetum brutiae*, was confused by various authors with *P. halepensis* or at best regarded as its variety. Lately, it has been accorded its deserved specific rank (Czeczott 1938), though some foresters continue to be vague about it. This species differs from *P. halepensis* not only in morphological characters, among which are its non-stipitated and non-pendulous ripe cones, but is also distinct in its ecological requirements which account for differences in its geographic distribution. *P. halepensis* is an Omni-Mediterranean, whereas *P. brutia* is an East-Mediterranean species. The distribution area of *P. brutia* comprises Chalcedonia, the Thassos islands, Asia Minor, Crete, Cyprus, the Lebanon, and a small enclave in the Iraqi Kurdistan (Zawita) and in northern Persia.

The spontaneous occurrence of *Pinetum halepensis* in Asia Minor has been contested by Papaioannou (1954), but Kayacik (1954) reports it from the Taurus, south-east of Ankara.

Where both species occur sympatrically, they differ in their edaphic requirements and in their tolerance to low temperatures.

The edaphic conditions under which each of these pine species grows naturally in various parts of their respective areas differ from country to country. Thus *Pinetum halepensis* is confined to sandy soils on the coast of southern Italy (Francini 1953) and in Greece (Philippon 1895, Pritzel 1908, Oberdorfer 1948), whereas it never occurs on sandy soils in the Lebanon or in Palestine. In Palestine natural *Pinetum halepensis* grows mostly on Cenomanian marls and chalks.

TABLE V

Analytical table of association Pinetum brutiae libanoticum

Number of record	26	27	28	Presence
Altitude in metres	900	900	1000	
Slope and exposure	SE15°	SE	—	
Height of <i>Pinus brutia</i> in metres	—	10-15	—	
General coverage	80%	90%	70%	
Surface in m ²	400	400	100	
CHARACTERISTIC OF ASSOCIATION				
<i>Pinus brutia</i>	1	2	2	3
CHARACTERISTICS OF ORDER QUERCETALIA CALLIPRINI				
ESPECIALLY FREQUENT IN PINETA				
<i>Juniperus oxycedrus</i>			1	1
<i>Cistus villosus</i>	2	3	1	3
<i>Cistus salvifolius</i>			2	1
CHARACTERISTICS OF ORDER QUERCETALIA CALLIPRINI				
AND CLASS QUERCETEA CALLIPRINI				
<i>Quercus calliprinos</i>	3	3	3	3
<i>Rhamnus palaestina</i>	2	2	1	3
<i>Calycotome villosa</i>	1	1	2	3
<i>Phlomis viscosa</i>		1		1
<i>Stachys distans</i>		1		1
<i>Smilax aspera</i>		+		1
<i>Rubia olivieri</i>		1		1
<i>Stipa bromoides</i>		2		1
<i>Dactylis glomerata</i>	+	2	+	3
<i>Poterium spinosum</i>	1	2	+	3
ACCIDENTALS				
<i>Ceratonia siliqua</i>		+		1
<i>Teucrium polium</i>		1		1
<i>Urginea maritima</i>	2			1

Pinetum brutiae is found on various siliceous and calcareous soils in Asia Minor (Schwarz 1936) and on igneous rocks of the Troodos Mountains in Cyprus (Holmboe 1913, and personal observation). In Southern Lebanon it seems to be confined to the areas where the Jurassic and Aptian strata outcrop on narrow strips of land, but it apparently avoids Cenomanian rocks. In Northern Lebanon, on the other hand, *Pinetum brutiae* has been observed on serpentine, and on marly chalks which apparently correspond to those on which *Pinetum halepensis* is found in Palestine. However, *Pinetum halepensis* has a lower elevation limit than *Pinetum brutiae*, at least in the Lebanon. In the Iraqi Kurdistan, *Pinetum brutiae* has been studied by the author together with A. Eig in Zawita (Dohouk distr.) where it appears on Eocene marly chalk and on hard Asmari limestone.

Throughout their areas, both *Pinetum halepensis* and *Pinetum brutiae* occupy rather restricted regions of specific rocks and soils. They are usually surrounded by comparatively large expanses of *Quercetum*, *Quercetum ilicis* in Italy and parts of Greece, *Quercetum calliprini* in Asia Minor, the Lebanon and Palestine, *Quercetum infectoriae* and *Quercetum brantii* (*persicae*) in Zawita.

Pinetum halepensis

After *Pinetum brutiae* had been found near Roûm in Southern Lebanon, the author searched for *Pinetum halepensis* throughout the later parts of her itinerary. In Southern Lebanon, at the elevation of 900–1200 m, no *Pinetum halepensis* was discovered. In Central Lebanon near Ain Traz, a single stand was found on Cenomanian marly chalk. The following record was noted:

<i>Pinus halepensis</i> 15–20 m high; young trees also found to occur.	
<i>Quercus calliprinos</i> , small	<i>Salvia triloba</i> , few, small
<i>Pistacia palaestina</i>	<i>Thymbra spicata</i>
<i>Rhamnus palaestina</i>	<i>Fumana thymifolia</i>
<i>Calycotome villosa</i> , numerous	<i>Majorana syriaca</i>
<i>Spartium junceum</i>	<i>Onosma frutescens</i>
<i>Hypericum serpyllifolium</i>	<i>Smilax aspera</i>
<i>Poterium spinosum</i>	

One large *Pinus halepensis* tree was found in a courtyard of the Moukhtarah village. When questioned on the tree, the owner of the house informed us that it had been sown 25 years earlier from seed received from near Damour. Damour is situated near the coast between Beirut and Sidon and lies within an area designated by Dubertret as Cenomanian. Inferring from an analogous situation in Northern Palestine, it may be assumed that *Pinetum halepensis* occurs south of Beirut on marly chalk of the large Cenomanian block (c₄ on Dubertret's map) at altitudes of less than 600 m mostly (Saida and Beirut sections of Dubertret's map of the Lebanon).

THE SPONTANEITY OF *Pinus pinea* FORESTS IN THE LEBANON

It is the common belief of botanists and foresters of our region that *P. pinea* forests are not spontaneous in the Lebanon. This belief stems no doubt from various competent sources of literature.

Mention must be made of Post (1889) first of all. In his geobotanical paper on Syria and Lebanon he wrote (p. 41): "*Pinus Pinea* L. is cultivated in open groves, rarely in dense forests, over a large portion of the outcropping sandstone spurs of Lebanon. ... It is little, if at all, cultivated in Antilebanon, seeming not to thrive far from the sea". In his Flora (1896) Post records "sand and rocky places" as the habitat of *P. pinea*, and further remarks: "extensively cultivated, and usually pruned to an umbrella-like top on a naked trunk". This remark leaves no doubt that Post did not consider *P. pinea* forests to be spontaneous in the Lebanon. Dinsmore, in the revised edition of Post's Flora (1933), added to the above remark: "probably originally from Asia Minor".

The opinion that *P. pinea* has been introduced into Lebanon is often connected with the name of the famous Druse Emir, Fakhr-ed-din.

As one of such sources quoting Fakhr-ed-din in connection with the pine forest near Beirut, Fraas (1876) will be quoted. Fraas, a geologist who gave a lively description of the Lebanon and of its wild vegetation, says: "If the substrate is sandstone or sandy soil, one is sure to expect that Pinea pines rise with their proud growth, and span their dark umbrella-roof at the height of 15-20 metres" (translated from the German text p. 61-62). And further: "Not to confound with the tree is *Pinus maritima*, which forms the so-called Pinea-forest of Beirut. One says that this, more properly, fir-forest had been planted by the Emir Fakhr-ed-din in the 17th century. Others held it for being much older, for a remnant of an old sacred grove". Fraas was mistaken about the identification of the pine in the forest south of Beirut. *P. maritima* does not occur in the Eastern Mediterranean and is recorded neither by Post nor by any later source from the Lebanon. This passage is quoted because of the last remark in particular, which hints at the possibility of the forest having been in existence prior to Fakhr-ed-din's times.

In an attempt to clarify the question of spontaneity of Pinea forests in the Lebanon, the present author thought that a looking into the history of Fakhr-ed-din, in order to find out the truth about that pine forest south of Beirut, was called for. Perusal of various sources (Carali 1936, Chebli 1946, Ismail 1955) revealed a fascinating piece of history of the Lebanon and of its most prominent ruler.

Fakhr-ed-din, Prince of Lebanon (1572-1635) was a strong personality, who fought most of his life against the Ottoman regime. He is noted for having achieved unity among religious groups of the Lebanese people and for having promoted the country's economic development. The following quotations from Ismail (1955) illustrate the modernizations introduced by Fakhr-ed-din, and also throw light on the point in question. The quotation (p. 100-101) refers to

the changes introduced by Fakhr-ed-din after his return from his five years' stay in southern Europe, mostly in Italy. "Dans l'exécution de son plan d'urbanisme l'Emir fit appel aux experts étrangers: à des Florentins... et des Français... Parmi le techniciens de Fakhr-ed-din figuraient: un médecin florentin: Matteo Naldi de Sienne, un médecin française... un architecte sculpteur: Cioli, un maître maçon: Fagni, un boulanger: Celini, un peintre français" (who is said to have painted for Fakhr-ed-din 1500 species of plants in colour). "Beyrouth avait été, jusque-là un vieux port négligé et malsain. Fakhr-ed-din fit de cette ville sa résidence d'hiver. Il la transforma en un jardin de plaisance... où de nombreux jardins à fleurs furent partout aménagés. Il fit planter tout autour une forêt de pins...". The last sentence is accompanied by the following footnote: "177. D'Arvieux, *Memoires* (1735) II, p. 333; Volney, *Voyage* II, p. 75 — Maundrell dit: en une demi-heure de Beyrouth... un petit bois de pins plantés par Faccardin... Maundrell, *Voyage d'Alep à Jérusalem à Pâques 1697*, p. 71. — Mariti raconte, d'autre part, que le sculpteur et architecte italien Cioli aménagea cette forêt en supprimant un grand nombre d'arbres pour permettre un alignement exact et il transforma les alentours en vergers fertiles. Cité par Carali, loc. cit. II, p. 154. — Il nous semble plus vraisemblable que Fakhr-ed-din ait seulement aménagé cette forêt qui existait déjà, car ni Khalidi ni Roger, qui vécurent à la cour de l'Emir, n'ont mentionné cette transformation".

This last sentence of Ismail thus goes to disprove the fact cited by various authors (D'Arvieux, Volney, Maundrell), all of whom lived after Fakhr-ed-din's execution by the Ottomans in 1635. Some of the historians note that the personality of Fakhr-ed-din has given rise to many legends, and that not all the deeds attributed to him are proved by documentary evidence.

Mariti (1787), mentioned in the above quoted passage from Ismail, literally says in connection with what Carali calls the famous and ancient pinetum of Beirut: "Cioli, to make it more regular and pleasant, had cut down all the maquis which surrounded the pines and grew among them, reduced the terrain underlying them to a meadow", etc. Carali (1936 p. 52) who cites Maundrell in connection with the plantation of the pine forest by Fakhr-ed-din also mentions that Pococke refuted that fact. The following passage from Pococke is cited here in German, since only the German edition of the book (1771) is available in Jerusalem, and the present author hesitates to translate back into English: "Etwa zwei Meilen von dieser Stadt (Beyrouth) kamen wir durch einen artigen Wald von Kiefern an dem Vorgebirge. Diesen Wald soll der berühmte Feckerdin mit eigener Hand gepflanzt haben. Doch scheint dies wohl irrig zu sein; denn er kommt schon in der Geschichte des heiligen Krieges bei der Belagerung von Beyrouth vor, wobei er den Christen sehr vortheilhaft gewesen sein soll". (§ 138 p. 131).

From the passages cited above it seems clear that the architect engaged by Fakhr-ed-din cleared only the underwood of the *Pinetum pineae* forest which grows on

the sandy soil south of Beirut up to this day. Search among the documents from Fakhr-ed-din's times assembled by Carali gave the present author no indication of pines being introduced from abroad, or of a forest actually being planted by Fakhr-ed-din. The management of the Beirut pine forest in the hands of a sculptor-architect could only have been its transformation into a park. Besides, planting of forests seems never have been practised in the Lebanon or Palestine before the later part of the 19th century. Moreover, architects are not generally known to plant forests!

On the other hand, one finds a detailed description by Maundrell (1697) of a well-planted and irrigated orange grove adjoining the magnificent palace of Fakhr-ed-din in Beirut. To sum up, the introduction of *Pinus pinea* into Lebanon by Fakhr-ed-din or somebody else is not proved by valid evidence.

P. pinea is found nowadays in the majority of the Mediterranean countries and, as was noted by Rikli (1912), it is not always possible to establish whether or not it is spontaneous in a particular locality. Nevertheless, floristic and phytosociological literature brings enough evidence of *P. pinea* growing wild in the following countries: Portugal, Spain, Corsica (Briquet 1910), the Tyrrhenian coast of Italy (Lüdi in Rikli 1946), Peloponnes in Greece (Philippson 1895, Pritzel 1908, Oberdorfer 1948) and the coast of Asia Minor (Krause 1916, Schwarz 1936, Davis 1949, Walter 1956). In North Africa *P. pinea* is recorded only as cultivated (Desfontaines 1799, Maire, Guinochet et Faurel 1952).

The vegetation of Asia Minor has recently been the subject of detailed investigations by several authors. All authors concerned mention *Pinetum pineae* as part of the natural vegetation of that region. There seems, therefore, no obvious reason, to accept a priori the opinion that the same forest type could not be spontaneous also in Lebanon. The fact that no *Pinetum pineae* occurs between the Central Lebanon and the southern shores of Asia Minor can be explained by the absence of suitable geologic formations all along this gap.

It is noteworthy that contrary to Post, Boissier (1884) apparently regarded *P. pinea* spontaneous in "Syria in regione litorali", while he recorded it as non-spontaneous from Crete.

The observations made by the present author in the *Pinea* forests of Lebanon convinced her that these forests represent an indigenous type of vegetation. The following evidence supports this contention:

(1) Phytosociological records taken in localities scattered over the main areas of *P. pinea* forests in the Lebanon showed a surprising constancy. Several associates invariably appear in the majority of the records (see Tables III and IV). Moreover, the floristic composition of this forest type in the Lebanon shows much resemblance to that of *Pinetum pineae* in Asia Minor (Schwarz 1936), where the spontaneity of *Pinea* forests seems not to be questioned nowadays.

(2) The essential uniformity of the specific edaphic conditions prevailing in

Pinetum pineae in Lebanon, which is often recorded in the botanical and geological literature (Post, Fraas, Diener, Dubertret), was confirmed in the records throughout this study. The natural relationship between this forest type and its habitat is strongly emphasized by abrupt changes in vegetation at points where these edaphic conditions happen to be replaced by others.

On a trip from Hammana to Douhour Choueir between Qornâyel and Bzebdine the author has been struck by a sudden change in vegetation on a turning of the road in a small ravine, where *Pinetum pineae* was suddenly replaced by a *Quercetum calliprini*. At this point, the sandstone adjoins an outcrop of the Cenomanian limestone. Similar changes in vegetation are known to the author also from Mt. Carmel where at various points *Pinetum halepensis* on a marly chalk adjoins a *Quercetum calliprini* where a hard limestone appears on the surface owing to a rift.

Mouterde (1947) remarks on *Pinus pinea* "on le trouve . . . généralement mais non exclusivement sur les terrains gréseux". Indeed, also the present author has found *P. pinea* on limestone in several localities. It was in the immediate proximity of larger villages, such as Djezzine, el Moukhtâra, Bâter. It appears that after the First World War the French authorities in the Lebanon induced farmers to plant new pine woods near their villages. Planting was often done on barren slopes which could not be used for fruit orchards. On the hard Cenomanian limestone above Djezzine the following notes were taken on 21.9.42: "A *P. pinea* grove on very stony ground of a hard grey limestone with some terra-rossa soil. *P. pinea* trees are close to each other, often only 1 m apart. The trees vary in size, some are 7-8 m high with trunks 10-15 cm in diameter, others are small and very slender. The accompanying vegetation is:

<i>Quercus calliprinos</i> numerous	<i>Psoralea bituminosa</i>
<i>Quercus infectoria</i> few	<i>Atractylis comosa</i>
<i>Rhamnus palaestina</i>	<i>A. serratuloides</i>
<i>Styrax officinalis</i>	<i>Carlina involucrata</i>
<i>Calycotome villosa</i>	<i>Dactylis glomerata</i>
<i>Cistus villosus</i>	<i>Stipa bromoides</i>
<i>Poterium spinosum</i>	<i>Lonicera etrusca</i>
<i>Majorana syriaca</i>	<i>Smilax aspera</i>
<i>Fumana arabica</i>	<i>Rubia olivieri</i>
<i>Onosma frutescens</i>	

Floristically, the presence of climbers, usually absent in *Pinetum pineae*, and the absence of the faithful *Juniperus oxycedrus* and *Lavandula stoechas* are remarkable. *Quercus calliprinos* is taller than is usual in *Pinetum pineae*, where it reaches this height only in ravines. The *P. pinea* trees seem not to be happy here".

In conclusion, it seems warranted that though one occasionally encounters plantations of *P. pinea* on limestone, this is not the natural habitat of that tree.

(3) During her visit to the Lebanon in 1942 the author, with the aid of Mr. A. Grizi, who speaks Arabic fluently, questioned a number of local inhabitants as to the indigeneity of *P. pinea* in the Lebanon. One of the inhabitants of Hammana directed us to a villager by name of Malhem Kossas in the village Bmariam (SW. of Hammana). The following notes were taken on the spot (23.9.42):

"Asked about the origin of a forest near and below the village, and on the practice of forest management, the villager replied that the forest was thousand and more years old; that it was tended already by his forefathers and that he did not think that the pines had been brought from somewhere, but that they had existed there from ancient times, at any rate before the times of Fakhr-ed-din. The majority of the trees in the forest in Bmariam are a hundred years old. It is usual to thin out the forest and to eliminate trees which do not bear fruit. Below the village, the villager showed us a tree growing on sandstone which he designated as being 200 years old. It was larger than most trees, and its diameter was 60–70 cm. The smaller trees around it were evidently self sown. Further we saw several other 200 years old trees. When asked about *Quercus infectoria* he said that it, too, was "from Allah, like the Snobâr (*Pinus pinea*)". Sometimes the soil between the pines is manured, and wheat is sown on terrassed soil. The villager furthermore took us down a hill to a place where a 500 years old tree 3.5 m in circumference was growing."

Summing up all the data collected, and in view of the lack of evidence as to the introduction of *P. pinea* by Fakhr-ed-din, the author feels justified in concluding that *Pinetum pineae* is a natural forest type spontaneous in the Lebanon.

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PROPHYLLS AS SEPALS IN ORCHIDACEAE

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ABSTRACT

It is generally accepted as a classical theory that the Orchids have no prophylls at all. This theory has been demonstrated to be erroneous. Studies of microtomic sections exhibit that the first formed leaves on the vegetative axis are two prophylls which are more or less connate. The first primordia in the flowers are two lateral leaves which develop into sepals, free or rarely united. The two lateral sepals of the orchid flower are the oldest and are thus the prophylls. In Gramineae and many other Monocotyledones the two-keeled dorsal prophylls are made up of two which are connate.

The classical morphologists of the last century knew that a dorsal and two-keeled prophyll was characteristic of most Monocotyledones. From this rule there were but few exceptions, among which the most important one is the largest of all families, the *Orchidaceae*, about which e.g. Eichler categorically declared that the flowers are completely without prophylls. This view has later been entered in the textbooks, where for more than a century it has been considered an incontestable fact.

If, however, this view should be correct, it would be reasonable to expect that the vegetative lateral shoots should also be without prophylls. In order to have this question decided I examined some North European species and found that in all these orchids there is now one, now even two (Figures 1-2) prophylls on the vegetative axes, completely as in grasses as well as most other Monocotyledones. After this discovery the possibility offered of having elucidated the old controversial question whether the solitary, dorsal, two-keeled prophyll does not actually consist of two, which have fused completely or in part.

In the search for prophylls in the flowers of orchids, the possibility must be considered that they may be suppressed so that they may still, perhaps, be present at an early stage of the development of the flower. Such stages therefore were examined in some different species, collected partly in nature, partly in a rich hot-house in the Botanical Garden of the University of Copenhagen.

In all the species examined the ontogeny appeared to be so uniform that it proved sufficient to depict a single species, *Oncidium varicosum* Lindl. To facilitate matters the same organs have been denoted with the same hatching and signs in the figures.

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The development of the flower is shown in Figures 3-7. It is seen that the primordium of the flower (Figure 3) is an axis A_2 in the axil of the bract D , on the relative main axis A_1 . The oldest leaf of the flower (Figure 4) is the sepal, a , which is always formed obliquely on the posterior side of A_2 , just as the first prophyll in the Dicotyledones. The oldest sepal but one, b (Figure 5), also appears obliquely 120° from a . In many other orchids (Figure 9) these two sepals are fused, and thus such a dorsal and two-keeled prophyll arises both in form and position like (and homologous with) the prophyll characteristic of most Monocotyledones. Indeed, $a+b$ are also homologous to the two transversal prophylls of the Dicotyledones.

The third sepal (c in Figure 6) is median and anterior. Only rarely (*Cryptochilus*) is c also fused with a and b .

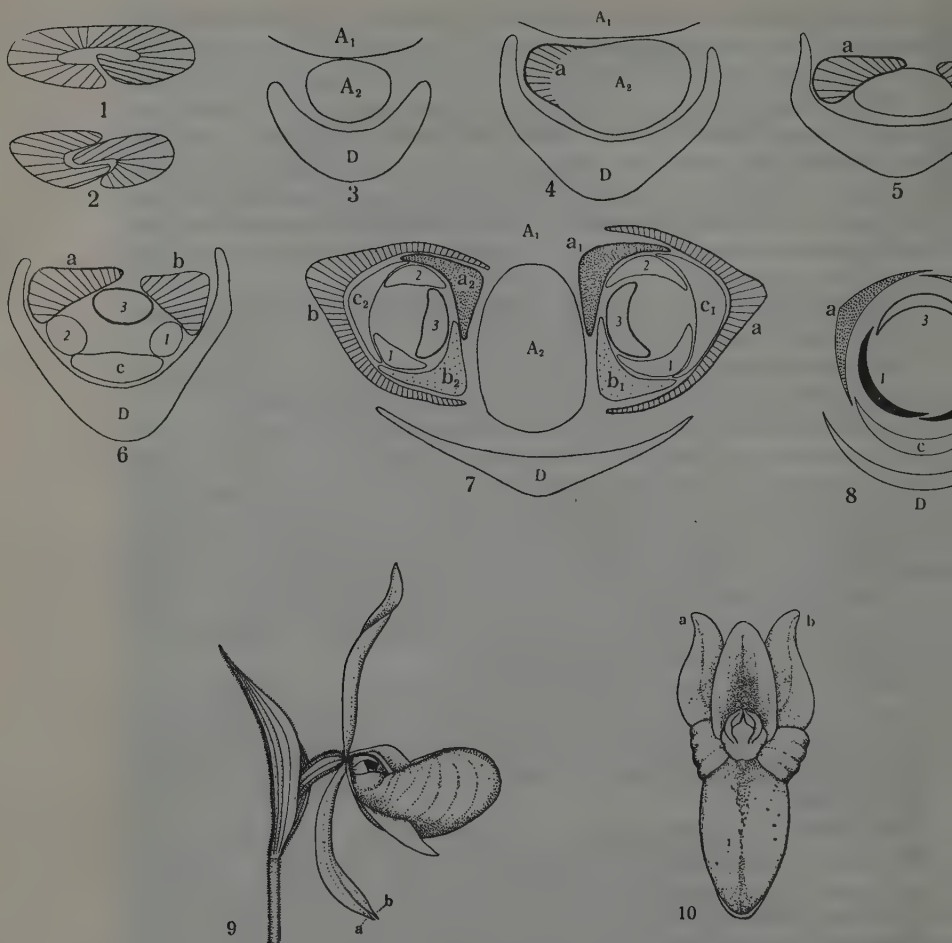
The primordia of the petals (1, 2, 3; Figure 6) appear in such a way that the latest one (3) is median and posterior and develops into the labellum.

That a and b are actually the prophylls of the flower, which form part of the calyx, appears not only from their development—as shown above—but also from the fact that a and b in some species can support an axial shoot, which later develops into a flower. This is seen in Figure 7, which shows that the two flowers that are supported by a and b are mutually antidromous, a_1 emerging on the right in one flower, but a_2 on the left in the other flower. As a also emerges from its axis (A_2) on the right, the flower of a is homodromous with the mother axis. These mutual relations within the phyllotaxis thus are also completely in agreement with the corresponding relations in the Dicotyledones.

If c also supports a flower, this will be in an anterior position. Furthermore, a_1 , a_2 , b_1 , b_2 in rare cases may also support flowers, and thus large ramose inflorescences arise. The best known examples of this are found within the genus of *Oncidium*, but instances also occur in other tropical genera, e.g. *Polystachya*, *Cyrtopodium*, and others.

The question then naturally arises whether strange double prophylls similar to those found in the *Orchidaceae* also occur in other Monocotyledones. This question can only be answered after a large number of further studies of such series of sections as have been used for the investigations described above. I have already studied some grasses, *Liliiflorae*, *Cyperaceae*, and found prophylls similar to those in *Orchidaceae*. In the near future I hope to be able to publish evidence showing that certain Gramineae have *two* mutually *free* prophylls, which may each have a bud in its axil. If only one bud develops within the double prophyll, this bud is *not* in a median position, but obliquely *lateral* to one keel of the prophyll, thus betraying its double nature.

These new facts will have wide consequences as regards the view on conditions of ramification in many Monocotyledones.



- Figures 1-2. *Epipactis helleborine*. Prophylls from vegetative lateral shoots. Figure 1. The prophylls fused at the posterior edges. $\times 45$. Figure 2. Two free prophylls. $\times 45$.
 Figures 3-5. *Oncidium varicosum*. Ontogeny of flower. The prophylls (a, b; hatched) initiated as independent organs. $\times 135$.
 Figures 6-7. *Oncidium varicosum*. Organogenesis of flowers. In the axil of the bract, D, issues the axis A₂, the prophylls of which, a and b, each support a flower with the respective prophylls a₁ and b₁, a₂ and b₂, which (together with c₁ and c₂) develop into sepals. $\times 45$.
 Figure 8. Orchidaceae. Typical diagram of the perianth. Prophylls (a + b) transformed into sepals. 3: labellum. For further details see text.
 Figure 9. *Cyripedium calceolus*. Prophylls a and b constitute two fused sepals. $\times 1$.
 Figure 10. *Malaxis paludosa*. Flower whose prophylls a and b have developed into sepals.

THE GENUS *MEDICAGO* L. IN LINNAEUS'S SPECIES PLANTARUM

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ABSTRACT

The part of the *Species Plantarum* dealing with the genus *Medicago* has been critically reviewed. Linnaeus's concept of *Medicago* and its subdivisions are discussed. The relevant material in the Linnaean herbaria, the Hortus Siccus Cliffortianus and the Linnaean Herbarium of the Linnaean Society of London have been examined. Based on the examination of specimens and the literature cited by Linnaeus, the genus *Medicago* L. and the nine species and thirteen varieties included by Linnaeus in it are typified. The inevitable changes in nomenclature affect three species, *M. polymorpha*, *M. turbinata* and *M. tornata*. In most varieties of *M. polymorpha*, which were later raised to the rank of species, the change of the author's name in current usage was found to be necessary. The typical intraspecific taxon of each subdivided species is established. It is shown that the type species of *Medicago* is *M. radiata* L. and not *M. sativa* L. as generally accepted. However, as the former species differs from all other species of *Medicago* in some important pod and seed characters, its separation from the genus *Medicago* and the conservation of the generic name *Medicago* L. are proposed.

INTRODUCTION

While engaged in a revision of the annual species of *Medicago*, we became interested in the Linnaean concept of the genus. It became clear to us that the nomenclatural confusion in that genus resulted to a great extent from the unfortunate treatment of it in the *Species Plantarum*. Every ambiguous phrase used by Linnaeus in the Sp. Pl. for describing a species or variety could subsequently cause their most different interpretations. This has been aggravated in *Medicago* by the fact that it is a widespread genus composed of very variable species.

It is most surprising that there is only seldom any discussion of Linnaeus's concept of a whole genus in botanical literature. The more, as there is no doubt that any information on Linnaeus's ideas on the nature of genera is of interest beyond the limits of the genus concerned. In the case of *Medicago*, however, some authors tried to elucidate Linnaeus's concept of, at least, part of the genus. Urban, the only monographer of *Medicago*, has published in 1883 (Urban 1883), ten years after the publication of his monograph (Urban 1873), the results of his examination of the specimens of *Medicago* in the Herbarium of the Linnaean Society of London. In that paper Urban added some notes on Linnaeus's concept of several varieties

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of *M. polymorpha*, not attempting, however, any typification, which was not practised at that time.

Recently Shinnars (1956) in Texas and Oostroom and Reichgelt (1957, 1958) in Holland made some important proposals as to the typification of the Linnaean taxa of the genus *Medicago*, though without examination of Linnaean specimens.

THE SPECIES AND THE VARIETIES OF THE GENUS *Medicago* IN LINNAEUS'S SPECIES PLANTARUM

In the Sp. Pl. nine species of *Medicago* are described, a small number in comparison with that described by most pre-Linnaean authors (Tournefort 1700, Morison 1680, etc.) and the post-Linnaean monographer—Urban (1873). Two of the Linnaean species, namely *M. virginica* and *M. circinnata* are referred by most later authors to *Lespedeza* and *Hymenocarpus* respectively, both not even belonging to the same tribe as *Medicago*—Trifoliae. A third species, *M. radiata*, is often regarded as *Trigonella* or *Pocockia*.

It seems obvious that Linnaeus classed his species with *Medicago* only on account of the shape of their pods ("legumen compressum longum inflexum".—Gen. Pl. ed. 5: p. 339, 1754) regardless of other criteria, such as characters of flowers or any vegetative characters.* Thus *M. circinnata*, for example, was included in the genus, though its leaves are strikingly different from those of all other species of *Medicago*.

None of the nine species is described by a new phrase-name. Six phrases are cited from the Hort. Cliff. (Linnaeus 1737), two of them with slight and one with essential alteration from the original; two phrases are from the Flora Suecica (Linnaeus 1745) and one from Gronovius's Flora Virginica (1739–1745).

The ninth species, *M. polymorpha*, cited from the Hort. Cliff. comprises thirteen varieties.** These correspond to 11 or 12 species according to most modern as also to most pre-Linnaean authors. The elevation of these varieties to the rank of species by post-Linnaean authors is one of the main causes of the nomenclatural confusions in *Medicago*. The species bearing Linnaeus's varietal epithets were attributed to Hudson (1762), Allioni (1785), Krockner (1790), Gaertner (1791), Desrousseaux (1791–1792) and Willdenow (1802). In each case the author, who has been the first to cite one of Linnaeus's varieties as a synonym, must be considered the author of the new combination (according to Art. 32 of the Intern. Code of Bot. Nomenclature 1956). This is so even in those cases, in which the diagnose or the type specimen are at variance with the correct identification of the Linnaean variety.

* Vegetative characters were as a rule not included in Linnaeus's diagnoses in the Genera Plantarum.

** The fourteenth variety, var. *nigra*, added by Linnaeus in the Mantissa Plantarum 2:454, is actually identical with the typical variety of *M. polymorpha*.

The reduction of species to varieties was often adopted by Linnaeus, and was criticized by some of his contemporaries (see Haller's letter to Linnaeus in App. 1). It should be stressed, however, that at least at the time of the compilation of the Sp. Pl., Linnaeus interpreted varieties not any more as somewhat vague entities, but regarded a variety as a "respectable taxonomic group, although not sufficiently well marked to be treated as a species" (cf. Sprague 1955).

In the case of the varieties of *M. polymorpha*, however, Linnaeus's concept seems to be different. There is much evidence to prove that Linnaeus had some prejudice against them and considered them as some queer, ill-defined and rather unimportant taxa as can be seen from the following:

(1) All the thirteen varieties of *M. polymorpha* are cited from pre-Linnaean authors, none being described by Linnaeus by a phrase of his own, and no habitat being added to any variety.

(2) The notes added after the enumeration of these varieties in the Hort. Cliff. and in the Sp. Pl. (ed. 2) also indicate that Linnaeus regarded these varieties as some queer "play of nature" not worth to be considered earnestly (see Linnaeus's remarks to this effect in App. 2).

(3) Of the thirteen varieties of *M. polymorpha*, four have the phrase-name and three a synonym cited from Morison (1680). With the exception of one variety, the phrase is cited together with the number of a figure in tab. 15 of Morison's book. Morison's excellent figures of pods for different species of *Medicago* are supposed to accompany, as in the case of all other genera, the description of the species bearing the same number. By an unfortunate accident, however, some of Morison's figures in tab. 15 were misplaced and consequently their numbers do not agree with the descriptions bearing the same numbers. Desrousseaux in Lamarck (1791-1792) was apparently the first to note this fact, because he cites the numbers of some of Morison's descriptions together with the correct number of the corresponding figures. Later Urban (1883) hinted at the way the figures should be arranged (for correct arrangement of the figures see App. 3).

Linnaeus, however, cites the phrase-names from Morison together with the figure marked by the same number as the description, disregarding the often striking disagreement between description and figure.

STUDY OF SPECIMENS IN THE LINNAEAN HERBARIA

In the course of this study we investigated the Hortus Siccus Cliffortianus of the British Museum and Linnaeus's Herbarium of the Linnaean Society* both in London. The type specimens of the taxa cited in the Sp. Pl. from the Hort. Cliff., without any or with irrelevant alterations, were expected to exist in the Hort. Sicc. Cliff. The types of other taxa were sought in the Linn. Herb. It should be stressed that a specimen, whose time of incorporation into the Linn. Herb. is not known,

* Abbreviated: Hort. Sicc. Cliff. and Linn. Herb. respectively.

cannot be assumed to be a type specimen, unless there is an indication that the specimen was in some way connected with the Sp. Pl. (compare Fuchs 1955, Stearn 1957). For instance, as Sauvages de La Croix gave his entire herbarium to Linnaeus in 1749 (Stearn 1957), any specimens of taxa cited in the Sp. Pl. from Sauvages (1751), which are marked as coming from Sauvages's collection, can be accepted as type specimens. However, the appearance on the herbarium sheet of the epithet written by Linnaeus's hand or of the same number as in the Sp. Pl., does not necessarily prove that the description in the Sp. Pl. has any connection with that certain specimen. If no special proof exists, there is no way of knowing if the specimen was not incorporated into Linnaeus's herbarium at a later date and determined by him according to the Sp. Pl.

In many cases, no connection could be traced between the phrase-name and any specimen, and so the actual type of the species or variety is an illustration in a pre-Linnaean publication cited by Linnaeus with any synonym of the phrase-name. In one case, there is no specimen in the Linnaean collections and no illustration is cited.

THE TYPE OF THE GENUS *Medicago*

M. sativa L. is generally thought to be the lectotype of the genus *Medicago*. This is in agreement with the very logical rule, accepted by most botanists, that the typical species of Linnaeus's genera are in most cases those species, having the epithet "officinalis", "vulgaris" or "sativus" (Hitchcock and Green 1929), as well as with Linnaeus's rule No. 246 in the *Critica Botanica* (1737).

However, in the case of the genus *Medicago*, this rule cannot apply. This was first noted by Scofield (1908), who pointed out that the name "Medicago" accepted by Linnaeus in the *Gen. Plant.* (1737) has its source from Tournefort (1700), and its type species is *M. radiata* L. according to Tournefort's illustration tab. 231.

In Tournefort's *Inst. Rei Herb.* two genera are described:

(1) "Medica" with 43 species, having "cochleae aemulum", typified on the upper part of his tab. 231 by an illustration of the species known at present as *Medicago scutellata* (L.) Mill.

(2) "Medicago" with four species, having pod "planum orbiculatum quasi falcatum", typified by the illustration of the species *Medicago radiata* L. at the bottom of tab. 231.

The generic name "Medica" was in use by most pre-Linnaean authors and was also adopted by Linnaeus as the name of the genus in the *Syst. Nat.* ed. 1 (1735). Subsequently, he changed the name of this compound genus to "Medicago" in the *Gen. Plant.* ed. 1 (1737), where he cites the name of the genus and the synonyms in the following order: *Medicago* Tournef., *Falcata* Riv., *Medica* Tournef., *Cochleata* Riv. This order of citation, apart from the acceptance of the name "Medi-

ago" instead of the much better known and more widely used name "Medica", bears witness to the fact that Linnaeus regarded the form with the falcate pod as the "typical" *Medicago* (typified by *M. radiata*). Therefore, *M. radiata* L. is to be accepted as the type species of the genus *Medicago* L.*

THE TYPES OF THE SPECIES OF THE GENUS *Medicago*

The following is an enumeration of the species of *Medicago* of the Sp. Pl. together with the typification of each species and remarks on the typification:

1. *Medicago arborea*. The phrase-name in the Sp. Pl. is cited with a slight alteration from the Hort. Cliff. In the latter, the phrase ends with "... caule frutescente", in the former with "... caule arboreo". This alteration can only be the result of observations in the field and not of examination of herbarium specimens, represented generally by a young branch. Therefore, the specimen "Hort. Sicc. Cliff. 377-6", accompanied by the phrase from the Hort. Cliff. on herbarium sheet should be considered the holotype.

2. *Medicago virginica* [= *Lespedeza virginica* (L.) Britt.]. The phrase-name is cited from Gronovius (1739). The type specimen might be preserved in the collection of J. Clayton in the British Museum (This collection was not seen by us).

3. *Medicago radiata* [= *Trigonella radiata* (L.) Boiss.]. The phrase-name is cited from the Hort. Cliff. without alteration. The specimen "Hort. Sicc. Cliff. 377-8", accompanied by the same phrase on the herbarium sheet, is the holotype.

4. *Medicago circinnata* [= *Hymenocarpus circinnatus* (L.) Savil.]. The phrase-name is cited from the Hort. Cliff. without alteration. The specimen "Hort. Sicc. Cliff. 377-7", accompanied by the same phrase on herbarium sheet, is the holotype.

5. *Medicago sativa*. The phrase-name is cited from the Hort. Cliff. with an alteration seeming at first unessential: "*Medicago pedunculis laxe spicatis*** leguminibus contortis caule erecto glabro" (Hortus Cliffortianus p. 377); "*Medicago pedunculis racemosis*** leguminibus contortis, caule erecto glabro" (Species Plantarum p. 778). Nevertheless, comparing the synonyms of the species in the Hort. Cliff. with those of *M. sativa* in the Sp. Pl., we see that the species of the Hort. Cliff. was split in the Sp. Pl. into *M. sativa* and *M. falcata*. The synonyms cited with *M. sativa* in the Sp. Pl. from Clusius, Morison and Lobelius, are identical with the synonyms of the var. δ of the species bearing the phrase-name cited above in the Hort. Cliff. However, the synonyms cited with *M. falcata*, namely from Bauhin (1623) and Clusius, are synonyms for the whole species (typical variety) of the Hort. Cliff.

Evidently, though Linnaeus cited in the Sp. Pl. the phrase from the Hort. Cliff.,

* Typotype (the specimen from which the drawing was made) might perhaps be preserved in the Herbarium of the Muséum National d'Histoire Naturelle in Paris, where some specimens of Tournefort are located.

** Author's italics.

he had changed greatly his concept of *M. sativa* since the publication of the Hort. Cliff. It is known (cf. Stearn 1957) that Linnaeus has not seen the Hort. Sicc. Cliff. after 1738. We may assume, therefore, that no specimen of that herbarium can be responsible for the change of his concept of *M. sativa*, and consequently, no specimen from the Hort. Sicc. Cliff. can be the type.

There are two specimens of *M. sativa* in the Linn. Herb., but they bear no indication of having any connection with the species described in the Sp. Pl.* Therefore, the lectotype can only be chosen among the illustrations doubtlessly seen by Linnaeus when describing *M. sativa*. We think that the figure of Morison, tab. 16 f.2 (1680), cited by Linnaeus in the Sp. Pl. and bearing the same epithet, is the most strongly connected with the species.

6. *Medicago falcata*. The relation of this species to *M. sativa* was discussed above. The phrase-name is cited from the Fl. Suec. No. 620 (p. 223), where Linnaeus states: "Habitat ad agrorum margines in Uplandia, Scania, Gotlandia passim". It is most possible that Linnaeus had a fair number of specimens of *M. falcata* in his herbarium. In the Linn. Herb., however, there are two specimens only, one—933-8—marked with "falcata 6", the other—933-9—with "6", none showing any connection with the Sp. Pl. or with the Fl. Suec. We believe, however, that some specimens might be found in one of the Linnaean collections in Sweden and refrain, therefore, from choosing any lectotype at present.

7. *Medicago lupulina*. The phrase-name is cited from the Fl. Suec. In its outer appearance this species is quite unlike any other species of the genus *Medicago* and was included in the Hort. Cliff. within the genus *Trifolium*. On transferring it to the genus *Medicago*, Linnaeus adhered to the phrase of the Hort. Cliff., changing only the name of the genus. Nevertheless, we cannot accept the specimen in the Hort. Sicc. Cliff. bearing the phrase as being the type, because the transfer of the species to another genus was doubtlessly based on additional specimens examined by Linnaeus after the completion of the Hort. Cliff. (as stated above, the specimens of the Hort. Sicc. Cliff. were not seen by Linnaeus after 1738).

The only specimen in the Linn. Herb. "933-10" bearing the name *M. lupulina* on the herbarium sheet, does not give any indication of being connected with the Sp. Pl. As in the case of *M. falcata* and for the same reason, we decided not to choose any lectotype at present.**

* "933-6" designated as "5 sativa" by Linnaeus gives no further indication in this regard. "933-7" is a specimen added to Linnaeus's herbarium at least as late as 1773, as can be deduced from having on it the collector's name Escallon (cf. Savage 1945).

** If no type specimen should be found, we could choose as the most plausible lectotype the figure of J. Bauhin and Cherler (1650-1651) p. 389 accompanying the description of "Trifolium pratense luteum mas, flore minore..." This source is cited by Tournefort as synonym to the phrase-name which Linnaeus cites as synonym in the Fl. Suec. for his later *M. lupulina*.

8. *Medicago marina*. The phrase-name is cited from the Hort. Cliff. with a slight alteration. Whereas it ends in the Hort. Cliff. with "... caule procumbente villosa",* it is changed in the Sp. Pl. to: "... caule procumbente tomentosum".*

Thus the specimen "Hort. Sicc. Cliff. 377-10" accompanied by the phrase from the Hort. Cliff. on the herbarium sheet is the holotype.

9. *Medicago polymorpha*. This species has thirteen varieties, their enumeration beginning with var. α , which has a certain significance (cf. Sprague 1955). The phrase-name is cited from the Hort. Cliff.: "*Medicago leguminibus cochleatis, stipulis dentatis caule diffuso*". One synonym only is added "*Trifolium cochleatum fructu nigro hispido*" from C. Bauhin's Pinax (1623).

The typification of this species poses a rather difficult problem. All the thirteen varieties were later raised to the rank of species and the specific epithet "*polymorpha*" was abandoned. Moreover, there are no specimens either in the Hort. Sicc. Cliff. or in the Linn. Herb. marked with that epithet on the herbarium sheet. It is possible, therefore, that the type may be a specimen of one of the thirteen varieties or still of another form not listed within these varieties.

The phrase of the cited synonym from the Pinax describes a smaller group of plants than the phrase describing *M. polymorpha*, the latter being a very accurate description of all the varieties included in the species. The phrase of the synonym, however, excludes from the species all spineless varieties and all those with pods not turning black at maturity. In the Hort. Cliff. the phrase from the Pinax is cited as a synonym of the variety ϑ of the species "*Medicago leguminibus cochleatis, etc.*" (11). This variety is described by a phrase cited from Morison, p. 154 (1680) "*Medica cochleata minor polycarpus annua capsula nigra hispidiore*".**

This same phrase from Morison is found on the label of one specimen—378-11 ϑ —in the Hort. Sicc. Cliff. The specimen belongs to the variety named var. *nigra* L. or var. *longeaculeata* Urb. of the species commonly known as *Medicago hispida* Gaertn. This seems to us to indicate a strong link between this specimen and the species called *M. polymorpha* in the Sp. Pl. Therefore, the type of *M. polymorpha* is the specimen "Hort. Sicc. Cliff. 378-11 ϑ ".***

It should be noted that Shinnars (1956) typified *M. polymorpha* also with the species known as *M. hispida* Gaertn., though he arrived at this conclusion without seeing any Linnaean specimens.

In conclusion, in this case typification compels us to depart from current usage and to change the epithet *M. hispida* Gaertn. to *M. polymorpha* L.

* Author's italics.

** This phrase is the synonym of the fourteenth variety of *M. polymorpha*—var. *nigra*—added by Linnaeus in the Mantissa.

*** In the two Linnaean herbaria seen by us there are some specimens of *M. polymorpha* (= *M. hispida* Gaertn.) though designated with the most different names or phrases.

THE TYPES OF THE VARIETIES OF *M. polymorpha*

Linnaeus's concept of varieties of *Medicago* as rather ill-defined taxa is also evident from his herbarium material. Among the specimens of *Medicago* species in both the herbaria examined, there is no clear mistake in the naming of the specimens. However, the case of the varieties of *M. polymorpha* is different. In the Linn. Herb. there are 12 herbarium sheets marked with the names of the numbers of the varieties in the Sp. Pl. or even with both in Linnaeus's hand. At least five of these are wrongly identified, and many varieties are not represented there at all. This suggests that the thirteen varieties of *M. polymorpha* were described by Linnaeus not from herbarium specimens but from literature.

The following is a list of the varieties together with their typification and the correct name of the taxon based on each variety as considered by us. Remarks on the typification and its consequence on present nomenclatural usage, are added.

Var. α *orbicularis* [= *Medicago orbicularis* (L.) Bart.].

The phrase-name is cited from Sauvages (1751). The holotype can, therefore, be only a specimen of Sauvages, and as Linnaeus received his entire collection, that specimen should be found in the Linn. Herb. However, the two specimens there, bearing the name "orbicularis" are not Sauvages's specimens.*

In the Hort. Cliff. this variety is described by a phrase from Morison (1680). In the Hort. Sicc. Cliff., however, the specimen labelled with the same phrase of Morison is a form of *M. polymorpha* (= *M. hispida* Gaertn.) with spineless pods which has a most superficial resemblance to var. *orbicularis*.

As lectotype, therefore, we chose the figure in Morison, 2: tab. 15 f. 1 (1680), because this illustration, which is cited in the Sp. Pl. as synonym for var. *orbicularis*, accompanies the phrase-name in the Hort. Cliff.

Var. β *scutellata* [= *Medicago scutellata* (L.) Mill.].

The phrase-name cited from Morison (1680) is the same as in the Hort. Cliff. No specimen of var. *scutellata* is to be found in the Hort. Sicc. Cliff. In the Linn. Herb. the only specimen—933-16—shows no indication of having any connection with the description in the Sp. Pl.

The holotype is the figure of Morison, 2: tab. 15, f. 3 (1680) (not f. 4 as cited in the Sp. P., see App. 2).

Var. γ *tornata* [= *Medicago tornata* (L.) Mill.].

The phrase-name "Medica tornata maior & minor lenis" is cited from Parkinson (1640). In this illustration the spineless and many-coiled pods of two different species are depicted: the single pod of "Medica tornata maior" belongs to the species usually named in botanical literature *M. turbinata* Willd. (considered by us

* "933-14", marked "orbicularis Alger" was according to Savage (1945) incorporated into Linnaeus's herbarium not earlier than 1756. "933-15" marked "a" shows no indication of any connection with Sauvages's type.

as *M. aculeata* Willd.); the group of pods of "*Medica tornata minor*" belongs to the species usually called *M. italica* (Mill.) Steud. or *M. obscura* Retz. (considered by us as *M. tornata** (L.) Mill.).

There are some indications to the fact that even though two different elements were included by Linnaeus in the variety, nevertheless he regarded "*Medica tornata minor*" as more typical:

(1) In the Hort. Cliff. the same source (Parkinson p. 1116) is cited but only as "*Medica tornata minor laevis*"** and a specimen of *M. tornata* (L.) Mill. is found in the Hort. Sicc. Cliff.—378-11 ♂—marked with this phrase.

(2) In the Sp. Pl. ed. 2 a description (not based on any pre-Linnaean author) is added after var. *tornata*: "Fructus plures subcylindrici anfractibus inermibus planis stipulae dentatae". This could describe only "*Medica tornata minor*" the only one of the two with "fructus plures", whereas "*tornata maior*" has never more than 1-2 pods on a peduncle.

(3) In the Linn. Herb. there is one specimen—933-17—marked "*Medica*" on top of the sheet and "*tornata*" on the bottom. This specimen is also a "*Medica tornata minor*".

As Linnaeus's concept of this variety changed between the completion of the Hort. Cliff. and that of the Sp. Pl., the type cannot be a specimen from the Hort. Sicc. Cliff. The only specimen in the Linn. Herb. marked with "*tornata*" might perhaps be a type specimen, as the name "*Medica*" on the herbarium sheet might bear some witness of its being incorporated into the herbarium at an early date. But as no further evidence to this effect exists, we had to choose as lectotype one of the two elements included in Parkinson's figure accompanying the phrase-name cited by Linnaeus: "*Medica tornata maior & minoris lenis*." The "*medica minor*" being considered more typical by Linnaeus, the figure of this element was accepted as lectotype (according to Intern. Code of Bot. Nomencl. 1956: Art. 10).

Var. ♂ *turbinata* [= *Medicago turbinata* (L.) All., syn. *M. tuberculata* Willd.].

This variety was first raised to the rank of a species by Allioni (1785). Allioni's concept of *M. turbinata* is not quite clear to us, but his citation of Linnaeus's variety as synonym from which he derived the specific epithet, makes Allioni's combination valid, as being based on Linnaeus's type.

Willdenow's *M. turbinata*, though also based on Linnaeus's var. *turbinata*, actually was considered by Willdenow, due to misidentification of the Linnaean variety, as part of the Linnaean var. *tornata*, the "*tornata maior*". The typification of

* It is puzzling that the epithet "*tornata*" almost completely disappeared from use and though the forms of this species with pods having few coils ($1\frac{1}{2}$ – $3\frac{1}{2}$) were united quite early, with those having 4–8 coils, nevertheless the name of the compound species in botanical literature remained *M. italica* or *M. obscura*. Oostroom and Reichgelt (1958) were perhaps the first to reinstate the epithet "*tornata*".

** *laevis* instead of *lenis* (author's italics).

Linnaeus's var. *turbinata*, on the other hand, leads to the conclusion that this variety is identical with the species known in botanical literature as *M. tuberculata* Willd.

In the Sp. Pl. the phrase-name is cited from Sauvages: "*Medicago fructu turbinato*". This phrase alone could describe different *Medicago* species. The cited synonyms, however, give a much clearer idea on Linnaeus's concept. These are from Morison (1680), J. Bauhin and Cherler (1650-1651) and C. Bauhin (1623). Morison's and J. Bauhin's phrases are each accompanied by an illustration, both doubtlessly showing the variety to be identical with *M. tuberculata* Willd. As there is no Linnaean specimen of var. *turbinata* to be found in both Linnaean herbaria, one of the two illustrations cited as synonyms by Linnaeus must be chosen as lectotype.

Morison's tab. 15, f. 6, which accompanies his phrase, cited in the Sp. Pl., is a very good illustration of the pod of the form with spineless pods within the species known as *M. tuberculata* Willd.* J. Bauhin's illustration, though showing a whole plant, is less explicit but also does not leave any doubt as to the identification. It excludes the possibility of being an illustration of the species known as *M. turbinata* Willd., because this species never has more than two flowers per peduncle, while the plant in the illustration has four to six, which is characteristic of the species known as *M. tuberculata* Willd. (cf. Urban, pp. 258-259, 1883).

As lectotype we chose among the two illustrations that of J. Bauhin. Sauvages cites it after the description of his species, and as Linnaeus accepted Sauvages's phrase-name for his var. *turbinata*, Bauhin's figure seems to us to be more closely linked with the Sp. Pl.

This typification compels us to change the name of the species known as *M. tuberculata* Willd. to *M. turbinata* (L.) All. The name of the species known as *M. turbinata* Willd., being a homonym, has to be changed into *M. aculeata* Willd.

Var. *ε intertexta* [= *Medicago intertexta* (L.) Mill.].

The phrase-name is cited from Morison (1680). The figures cited by Linnaeus together with the phrase are tab. 15 f. 8, 9, 7**. The figures accompanying the phrase are 8 and 9 (two aspects of the same pod); figure 7, depicting a pod very much alike that on figure 8, was added as synonym by Linnaeus. No Linnaean specimens of this variety, which should be taken into account, are known to us.***

* Though the case of *M. polymorpha* var. *turbinata* is the only one in the genus *Medicago* where Linnaeus cites one of Morison's descriptions without citing the figure to it, nevertheless, to our opinion, this is only an unintended omission, and at least it certainly does not mean that Linnaeus did not accept the figure as typical for his variety.

** The original sequence of numbers in the Sp. Pl.

*** In the Hort. Sicc. Cliff. the only specimen of this variety is labelled with a different phrase than Morison's. The specimen in the Linn. Herb.—933-18—is from about 1756 (cf. Savage 1945).

Therefore, Morison, 2: tab. 15. fig. 8 & 9 (1680), should be accepted as the holotype.

Var. ξ *arabica* [= *M. arabica* (L.) Huds.].

The phrase-name is cited from Morison (1680). It is accompanied by tab. 15, fig. 17 (to be changed to fig. 12; cf. App. 3). The synonyms are from Camerarius's Hortus Medicus (1588; not seen by us) and C. Bauhin (1623). Bauhin's conception is in full agreement with that of Morison.

The only specimen named "arabica" in the Linn. Herb.—933-24— is a specimen of Linnaeus's *M. polymorpha* var. *ciliaris*. As this is clearly a case of mislabelling, this specimen should be disregarded.

The holotype can, therefore, be only the figure of Morison, 2: tab. 15 f. 12 (1680).

Var. η *coronata* [= *M. coronata* (L.) Bart.].

The phrase-name cited from Sauvages is a fairly clear description of the variety. The synonyms cited from Morison (1680)*, C. Bauhin (1620, 1623) and J. Bauhin and Cherler (1650-1651) clearly describe the same variety.

In the Linn. Herb. the specimen—933-9— labelled "*coronata*", is a specimen of *M. polymorpha* L. emend Shin. Sheet numbered 933-20, however, labelled "*rigidula*" is a specimen of var. *coronata*. In this case, too, both specimens should be disregarded.

As lectotype we therefore, chose the figure accompanying the phrase "*Medica coronata cherleri parva*" in J. Bauhin and Cherler, 2: p. 386 (1650-1651), because "*Medica coronata Cherler*" is cited by Sauvages as the synonym for his phrase.

Var. θ *ciliaris* [= *M. intertexta* (L.) var. *ciliaris* (L.) comb. nov.].

The phrase-name is cited from Sauvages. Neither this phrase nor the synonyms which are from Tournefort (1700) and Magnol (1686) are accompanied by any illustration. There is, nevertheless, no doubt as to the identity of the described taxon.**

In the Linn. Herb. there is only one specimen of this variety—923-24— erroneously named *Medica arabica*. Therefore, there is neither a specimen nor an illustration which can be accepted as the type.

Var. ι *hirsuta* [= *M. minima* (L.) Bart.].

The phrase-name is cited from Sauvages (1751), the synonyms from J. Bauhin

* The figure marked by the same number as the description and, therefore, cited with it by Linnaeus, is fig. 21 on tab. 15 instead of fig. 16 (see App. 3). Gaertner (1791), who accepted the figures exactly as cited by Linnaeus, based his "*Medicago coronata*" and his illustration (tab. 155) on Morison's fig. 21, bringing about a great deal of confusion in later botanical literature.

** Var. *ciliaris* is the only known form of *Medicago*, except the much later described *M. lanigera* Winkl. et Fedtsch., a species endemic to central Asia, to which Tournefort's description "*fructu ciliari*" could be applied.

and Cherler (1650–1651) and C. Bauhin (1623). Only the phrase “*Medica echinata hirsuta*” cited from J. Bauhin is accompanied by an illustration. This phrase is also cited by Sauvages as synonym to his phrase.

There are no specimens of this variety to be found in the Linnaean herbaria studied. Therefore, the figure cited above in J. Bauhin and Cherler, 2:386 (1650–1651) was chosen as the lectotype.

This variety is very closely related to one of the following—var. λ *minima*—and is included by all post-Linnaean authors in *M. minima* (L.) Bart., a species based on var. *minima*.

Var. κ *rigidula* [= *M. rigidula* (L.) All.].

The phrase-name cited from Dalibard (1749) and the synonyms from J. Bauhin and Cherler (1650–1651) and C. Bauhin (1623), together with habitat-data and the illustration of J. Bauhin, make it obvious that var. *rigidula* is in fact identical with the species known in common usage as *M. rigidula* Desr.*

To my knowledge, no specimens of Dalibard exist in any herbarium. In the Linn. Herb. there is one specimen of *M. polymorpha* var. *coronata* L. named var. *rigidula*. As these two species are so distinctly different, this is a clear case of mislabelling.

The lectotype is the illustration from J. Bauhin and Cherler, 2: 386 (1650–1651) attached to the phrase “*Medica hirsuta echinis rigidioribus*”, cited as synonym by Dalibard for his species and by Linnaeus for his var. *rigidula*.

Var. λ *minima* [= *M. minima* (L.) Bart.].

The phrase-name cited from Guettard (1747) is a rather clear description. The synonyms are from J. Bauhin and Cherler (1650–1651) and from C. Bauhin (1623). To our knowledge no specimens of Guettard exist and also no specimens of var. *minima* were found by us in Linnaean herbaria.

We chose, therefore, as the lectotype the illustration in J. Bauhin and Cherler, 2: 386 (1650–1651) accompanying the phrase “*Medica echinata minima*”.

Var. μ *muricata* [= *M. rigidula* (L.) All.?.].

The phrase-name is cited from Morison (1680) together with reference to Morison's figure 11 of tab. 15 (to be changed to fig. 18—cf. App. 3) which is of course the holotype of the variety. Linnaeus does not cite any synonyms of this variety in the Sp. Pl.

From Morison's description, collection data and figure we deduced that var. *muricata* and var. *rigidula*, both varieties of *M. polymorpha*, are identical.

Var. *muricata* was raised to the rank of species by various authors after Linnaeus. The commonly used combination is that of Willdenow (1802). However,

* This change of rank of var. *rigidula* to *M. rigidula* should be attributed to Allioni (1785) and not, as commonly done, to Desrousseaux in Lamarck (1791–1792).

M. muricata Willd. is based on Morison's misquoted illustration, f. 11, which depicts *M. carstiensis* Jaqu. and was interpreted by Willdenow, as can be judged from his description and herbarium material, as one of the forms of *M. tornata* (L.) Mill. having spiny pods.

In the Linn. Herb. there is one specimen—933-21—labelled by Linnaeus "*muricata*". This herbarium sheet contains one of the forms of the species known as *M. tuberculata* Willd. having spiny pods. Apparently this is yet another example of mislabelling in the Linn. Herb.

Var. *v laciniata* [= *M. laciniata* (L.) Mill.].

The phrase-name is cited from Sauvages (1751), and synonyms, each with the accompanying illustration, from Magnol (1686) and Breyne (1678). One specimen of this variety is in the Hort. Sicc. Cliff. labelled with a phrase not cited in the Hort. Cliff. nor in the Sp. Pl. The only specimen of the variety in the Linn. Herb.—933-25—is, according to Smith's writing on the herbarium sheet, from Banks's herbarium. Therefore, neither can be considered as type specimen.

The illustration chosen as lectotype is t. 34 in Breyne (1678). We preferred it to that from Magnol, because Breyne's figure is cited by Sauvages and also var. *laciniata* is described in the Hort. Cliff. with Breyne's phrase-name.

DISCUSSION

The genus *Medicago* contains a great number of species, each with a wide range of variability. In the Sp. Pl. many of these species were regarded as varieties. The taxonomist who investigates the range of variability of each of them is often at a loss as to the exact characters of the "typical" variety or subspecies, especially where its type is (as in most cases of the genus *Medicago*) an illustration which is sometimes rather obscure and presenting often a pod only.

The names of the species of *Medicago* and their typical intraspecific taxa are given in Table I where they are compared with the names of the same taxa as accepted by Urban (1873). The typical intraspecific taxon of the species repeats the epithet of the species, and its name is, therefore, not cited in Table I. In three cases the epithet of the species has to be changed in order to bring it into agreement with the type. In most Linnaean varieties of *Medicago* the typification involves change of the author who raised the variety to the rank of species. For it should be kept in mind that if the variety is clearly defined, the first author who named a new species, citing Linnaeus's variety as synonym, must automatically be accepted as the author of the new combination.

The most far reaching nomenclatural consequence of the typification is that concerning the name of the genus. As mentioned, the type-species of the genus *Medicago* is *M. radiata*. Yet to our opinion this species should be excluded from *Medicago* as being distinct from other species of the genus in several significant

TABLE I

The species and varieties of Medicago in the Sp. Pl., their identification and the typical intraspecific taxa of the species

Name of the taxon in the Sp. Pl. (1753)	Name accepted by Urban (1873)	Name accepted by present author	The intraspecific taxon considered ty- pical by present author (name in Urban 1873)
<i>M. arborea</i>	<i>M. arborea</i> L.	<i>Medicago</i> (?) <i>arborea</i> L.	—
<i>M. virginica</i>	—	<i>Lespedeza virginica</i> (L.) Brit.	—
<i>M. radiata</i>	<i>M. radiata</i> L.	<i>Trigonella</i> (?) <i>radiata</i> (L.) Boiss.	—
<i>M. circinnata</i>	—	<i>Hymenocarpus cir- cinnatus</i> (L.) Savi	—
<i>M. sativa</i>	<i>M. sativa</i> (L.) Döll.	<i>M. sativa</i> L.	ssp. <i>macrocarpa</i> Urb. var. <i>vulgaris</i> Urb.
<i>M. falcata</i>	<i>M. falcata</i> L.	<i>M. falcata</i> L.	—
<i>M. lupulina</i>	<i>M. lupulina</i> L.	<i>M. lupulina</i> L.	var. <i>typica</i> Urb.
<i>M. marina</i>	<i>M. marina</i> L.	<i>M. marina</i> L.	—
<i>M. polymorpha</i>	<i>M. hispida</i> Gaertn.	<i>M. polymorpha</i> L.	ssp. <i>macrocarpa</i> Urb. var. <i>pentacycla</i> Urb. f. <i>longeaculeata</i> Urb.
<i>M. polymorpha</i> var. <i>orbicularis</i>	<i>M. orbicularis</i> (L.) All.	<i>M. orbicularis</i> (L.) Bart.	var. <i>marginata</i> (Willd.) Benth.
<i>M. polymorpha</i> var. <i>scutellata</i>	<i>M. scutellata</i> (L.) All.	<i>M. scutellata</i> (L.) Mill.	—
<i>M. polymorpha</i> var. <i>tornata</i>	<i>M. obscura</i> Retz.	<i>M. tornata</i> (L.) Mill.	ssp. <i>tornata</i> Willd. var. <i>inermis</i> Urb.
<i>M. polymorpha</i> var. <i>turbinata</i>	<i>M. tuberculata</i> Willd.	<i>M. turbinata</i> (L.) All.	var. <i>vulgaris</i> Urb.
<i>M. polymorpha</i> var. <i>intertexta</i>	<i>M. intertexta</i> (L.) Gaertn.	<i>M. intertexta</i> (L.) Mill.	ssp. <i>aculeata</i> Urb. var. <i>panormitana</i> (Ten.) Urb.
<i>M. polymorpha</i> var. <i>arabica</i>	<i>M. arabica</i> (L.) All.	<i>M. arabica</i> (L.) Huds.	—
<i>M. polymorpha</i> var. <i>coronata</i>	<i>M. coronata</i> (L.) Desr.	<i>M. coronata</i> (L.) Bart.	—
<i>M. polymorpha</i> var. <i>ciliaris</i>	<i>M. ciliaris</i> Willd.	<i>M. intertexta</i> (L.) Mill. var. <i>ciliaris</i> (L.) comb. nov.	—
<i>M. polymorpha</i> var. <i>hirsuta</i>	<i>M. minima</i> (L.) Bart.	<i>M. minima</i> (L.) Bart. [= <i>M. hirsuta</i> (L.) All.]	var. <i>vulgaris</i> Urb.
<i>M. polymorpha</i> var. <i>rigidula</i>	<i>M. rigidula</i> (L.) Desr.	<i>M. rigidula</i> (L.)	—
<i>M. polymorpha</i> var. <i>minima</i>	<i>M. minima</i> (L.) Bart.	<i>M. minima</i> (L.) Bart.	var. <i>vulgaris</i> Urb.
<i>M. polymorpha</i> var. <i>muricata</i>	<i>M. rigidula</i> (L.) Desr.	<i>M. rigidula</i> All. [= <i>M. muricata</i> (L.) All.]	—
<i>M. polymorpha</i> var. <i>laciniata</i>	<i>M. laciniata</i> (L.) All.	<i>M. laciniata</i> (L.) Mill.	var. <i>longispina</i> Benth.

characters and showing on the other hand strong links with some species included in the genus *Trigonella*. Various authors were in doubt whether *M. radiata* should be classed within *Medicago* or *Trigonella*. Urban (1873) included *M. radiata* within *Medicago*, because its cotyledons are without petioles like those of all known species of *Medicago*. Most known species of *Trigonella*, however, have cotyledons with petioles. This clear way of distinction seemed rather convenient and was adopted from that time by most authors dealing with both genera. Sirjaev (1933), the monographer of *Trigonella*, used this single character for transferring a number of species from *Trigonella* to *Medicago*, such as: *T. hybrida* Pourr., *T. ovalis* Boiss., *T. platycarpus* L., *T. cretacea* Tal., *T. plicata* Boiss. and others.

However, the adoption of this way of delimitation subsequently caused much confusion. Species having pods which are in no way similar to those of other *Medicago* species, but are very much like those of *Trigonella*, were thereby included within *Medicago*.

The pods of *M. radiata* are very much like those of *Trigonella arabica* and some other related *Trigonella* species (see Figures 1 and 2), but do not resemble those of any species of *Medicago*. No species of *Medicago* has pods with any protuberance on the ventral suture. The "spines" protruding from the dorsal suture, being superficial emergences only, are not homologous with those often occurring in *Medicago*, but exactly alike those in *Trigonella arabica*. Moreover, the seeds of *M. radiata* also differ from those of the genus *Medicago* (Figure 3).*

The facts shown above give rise to doubts as to the value of the single character chosen by Urban for the delimitation of both genera. Though we wish to refrain at present from any decision whether *M. radiata* should be transferred to *Trigonella* or be classed together with a group of closely related species of *Trigonella* as a separate genus (perhaps *Pocockia* Ser.), in any case the removal of *M. radiata*—the type species of the genus *Medicago*—to another genus involves the removal of the generic name together with the type species and brings about the change of the name of the residue of the genus (Intern. Code of Bot. Nomencl. 1956: Art. 52).

However, the change of the generic name of the genus *Medicago* would lead to much inconvenience (especially as *Medicago* is very widespread and some of the most important forage crops are included in it). We, therefore, propose to retain the name *Medicago* for the residue of the genus by including it in the list of nomina conservanda.

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* The seeds of *M. orbicularis* (L.) Bart., the only seeds much alike those of *M. radiata* in shape, differ in the character of the seed coat.



Figure 1

Pods of "*Medicago*" *radiata* L. showing diverse degrees of coiling. $\times 1\frac{1}{2}$. (Population from Israel, Negev, El Megera)



Figure 2

Pods of: 1. "*Medicago*" *radiata* L.; 2. *Trigonella arabica* Del.; 3. *T. schlumbergeri* Boiss.; 4. *T. graeca* Boiss. $\times 1\frac{1}{2}$.

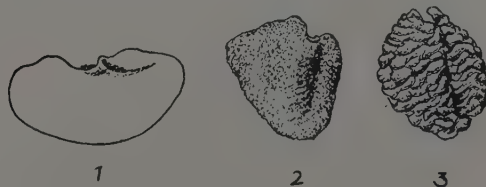


Figure 3

Seeds of: 1. *Medicago polymorpha* L. emend. Shin.; 2. *M. orbicularis* (L.) Bart.; 3. "*Medicago*" *radiata* L. $\times 6$.

various sources, and Dr. J. Lorch of the Hebrew University for his assistance in the preparation of the manuscript. The author's visit to the Linnaean Herbaria has been made possible by a generous grant to the Hebrew University by Mr. A. Bronfman.

APPENDIX 1.

Haller's letter to Linnaeus 17. Oct. 1748; Transl. Smith, Select. Corr. Linnaeus 2: 431. 1821. "Do not strike out species, and reduce them to varieties, so frequently as you accustomed... cannot, without concern, see good and genuine plants perish, as it were, and become lost to botanists, under the title of varieties".

Cited from Webster (1956) p. 5.

APPENDIX 2.

(1) Linnaeus, *Hortus Cliffortianus* 1737.

"Variat magnitudine totius plantae, fructus copiâ, figurâ, spinis cujus varietates si quis desideret, adeat Ray hist. 961 Moris, hist. 2 s. 2, f. 1-21. sed quis omnes recensere queat ubi natura varietate ludere et sense oblectare gestiat".

(2) Linnaeus, *Species Plantarum* ed. 2. 1763.

"Varietates hujus numerosae vix limites admittunt. In Cochleus hic provocavit polymorpha Natura Floram in certamen cum Fauna".

APPENDIX 3.

The figure numbers 1-21 in Morison, *Plantarum Historia Universalis* 2: tab. 15 (1680) should accompany the description of the genus *Medica* on p. 152-155 in the following order:

To description	1 figure	1	To description	12 figure	19
" "	2	2	" "	13	20
" "	3	4	" "	14	21
" "	4	3	" "	15	10
" "	5	5	" "	16	11
" "	6	6	" "	17	12
" "	7	7	" "	18	13
" "	8	8	" "	19	14
" "	9	9	" "	20	15
" "	10	17	" "	21	16
" "	11	18			

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GERMINATION-REGULATING MECHANISMS IN SOME DESERT SEEDS

VI. *CONVOLVULUS LANATUS* VAHL, *CONVOLVULUS NEGEVENSIS* ZOH. AND *CONVOLVULUS SECUNDUS* DESR.*

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ABSTRACT

Seed germination of *Convolvulus lanatus*, *C. negevensis* and *C. secundus* is regulated by a water-impermeable seed coat. Permeability is apparently attained by removal or dislodging of a small plug-like structure in the micropylar region of the seed coat.

Permeable seeds had high germinability between 20° and 30°C, in both light and dark. Prolonged dry storage of permeable seeds did not affect their germination. Germination did not take place at low temperatures (5°–7°C), but seeds thus treated germinated promptly upon transfer to higher temperatures.

Small scale experimental reseeding with *C. lanatus* and *C. negevensis* in their native habitat was successful in several instances, considerable establishment having taken place without any supplementary irrigation.

The three *Convolvulus* species are dwarf-shrubs growing in semi-arrested sands. *Convolvulus lanatus* belongs to the Saharo-Sindian phytogeographical element (Eig 1931–32), and is found in the deserts of southern Israel. It is considered a promising pasture plant for sandy soils of arid regions with 100–150 mm mean annual rainfall (Boyko 1949). *C. negevensis* Zoh. (inedit.) is a new species (M. Zohary, personal communication), found under similar climatic and edaphic conditions in Meishor Yemin (Tureibeh) in the central Negev, and is heavily grazed by livestock. *C. secundus* belongs to the East-Mediterranean element, and is found in coastal sands with 200–600 mm rainfall (Eig 1931–32).

Native pastures in most Middle-Eastern deserts have been heavily overgrazed. Natural regeneration under the existing arid conditions is an extremely slow process. Reseeding with native species for pasture purposes is, therefore, contemplated. This research was undertaken as an aid to the reseeding program.

MATERIAL AND METHODS

Seeds were collected from the natural habitat of the three species in June 1954 and 1955 (Mature seed could be collected during a very short period, as it is shed soon after maturity and disappears in the sand).

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Germination was carried out in Petri dishes containing filter paper moistened with tap water, or in flower pots containing sand from the natural habitat.

Most of the tests were carried out in illuminated incubators. Dark germination was carried out by placing the Petri dishes in light-tight cans.

RESULTS

Most of the work was done with *C. lanatus*, as its seeds could more readily be obtained. The pertinent tests were repeated with the other two species, which proved to behave and respond like *C. lanatus*. For the sake of conciseness, the results will be mostly cited for *C. lanatus*.

Seeds were germinated in both continuous light and dark at 20°, 26° and 30°C, respectively. In no case did *C. lanatus* and *C. negevensis* give more than 2%, and *C. secundus* more than 20% germination within two weeks. Since none of the ungerminated seeds had swelled, the seed coats were treated by various means. Mechanical scarification with sand-paper, or a careful needle-prick reduced the percentage of non-swelling seeds to 0-5%. Table I summarizes the effects of other seed coat-softening treatments on imbibition and subsequent germination of *C. lanatus* at 26°C in the dark. These treatments consisted of "impaction" (shaking the seeds vigorously in a glass jar by means of a mechanical bottle-shaker, cf. Hamly 1932) with and without sand; pre-soaking in absolute ethanol (cf. Verschaffelt 1912); treatment with concentrated H_2SO_4 (at 26°C). After the latter treatment the seeds were thoroughly washed and dried on blotters at 26°C.

TABLE I

Effectiveness of various seed coat-softening treatments on permeability and subsequent germination of seeds of *Convolvulus lanatus*, at 26°C in the dark
(Swelling percentages are given in brackets. Two replications, 50 seeds each, per test)

Treatment	Duration	Counts made on				
		2nd day	3rd day	5th day	7th day	9th day
Concentrated sulphuric acid	10 mins.	0 (6)	8 (12)	8 (12)	12 (12)	12 (12)
	30 mins.	26 (58)	46 (67)	67 (72)	78 (84)	84 (84)
	60 mins.	63 (87)	83 (90)	90 (90)	90 (90)	90 (90)
	90 mins.	—	82 (86)	86 (86)	—	—
Impaction with sand	1 hour	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	2 hours	0 (4)	4 (4)	4 (4)	4 (4)	4 (4)
	4 hours	0 (0)	0 (0)	0 (0)	12 (88)	88 (92)
Impaction without sand	1 hour	4 (20)	8 (20)	20 (28)	28 (32)	40 (40)
	2 hours	16 (36)	24 (36)	36 (40)	44 (44)	44 (44)
	4 hours	64 (88)	84 (88)	88 (96)	94 (96)	94 (96)
Absolute ethanol	5 days	0 (0)	0 (4)	4 (20)	12 (28)	20 (28)
Untreated controls	— — — —	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Other experiments showed that exposing the seeds to 50°–60°C dry heat, for as long as 70 hours, affected neither their impermeability nor their viability. Seeds thus treated were still impermeable, but when their coats were punctured they attained 90–95% permeability and germinability.

The site of water entry into the permeable seeds was investigated by embedding various parts of the seed coat in a water repellent, such as vaseline or plasticine (Koller and Negbi 1955). The seeds of all three species have a small depression on one of their tips, which corresponds to the micropyle. This tip will be referred to as the micropylar tip. It was found that such embedding of the micropylar tip of impaction-treated (hence permeable) seeds reduced their swelling percentage (e.g. 77%) to that of the non-impacted (impermeable) controls (0%). Embedding the opposite tip gave similar swelling percentages to those of unembedded, impacted (permeable) seeds (e.g. 75%).

Similar experiments, with acid-treated seeds, also resulted in a larger percentage of swelling when the micropylar tip was unembedded (Table II). However, acid-treated seeds, differed from impacted ones in having a considerable percentage of swelling despite an embedded micropylar tip.

TABLE II

Determination of the site of water entry into acid-treated seeds
(Figures represent swelling percentages after two days imbibition at 26°C)

	Duration of treatment	Untreated controls	Whole seed in water	Micropylar tip in vaseline	Opposite tip in vaseline
<i>G. lanatus</i>	80 minutes	0	90	48	78
<i>G. negevensis</i>	65 minutes	2	71	43	71
<i>G. secundus</i>	70 minutes	16	90	18	87

Freehand longisections disclosed that in intact seeds the bottom of the micropylar depression is lined with a distinctly shaped plug structure. This plug was absent from comparable sections of acid-treated seeds, obviously being more susceptible to acid than the rest of the seed coat.

Germination tests were carried out with seeds which had been subjected to sulphuric acid treatment (98% acid at 26°C for 75 minutes). 77.3% of the 700 seeds which were treated had become permeable. Nearly all permeable seeds thus obtained were found capable of rapid germination under all the temperatures (20°, 26° and 30°C), in both light and darkness. The mean germination percentage for all six sets of conditions was 97.7 ± 1.0 (S.D. = ± 2.5), within four days from sowing.

Further germination tests were carried out with acid-treated seeds which were dry-stored after treatment at 26° and 30°C in open containers for various periods, up to 28 days, prior to testing. The tests were carried out at 20° and 30°C, respectively. Under the above conditions the mean germination percentage of all tests

was 96.0 ± 1.3 (S.D. = ± 3.0), within four days from sowing, and rate of germination was practically unchanged. One lot of acid-treated seeds was tested after 12 months dry storage and still showed no change in germinability.

At low temperatures (5° – 7°C), acid-treated seeds imbibed freely when placed in water, but failed to germinate (at least during thirteen days). However, upon transfer to a higher temperature (20°C), 99% of the permeable seeds germinated within 48 hours.

After a series of successful pot experiments, to determine emergence of acid-treated seeds and the subsequent vigour of the seedling, a small scale reseeding test was undertaken under field conditions. This was done in the sands south of Beersheva, and in those of Meishor Yemin*, with acid-treated seeds of *C. lanatus* and *C. negevensis*.

The seeds were planted after a rain, on January 8, 1955, at a depth of 4–7 cm, and each seed was watered with one-half cupful of water to restore soil structure. No further irrigation was given hence, so that all subsequent seedling growth depended entirely on the naturally available moisture. When inspected (on February 18 and March 10, 1955) an overall emergence of 60–65% was found in most of the experimental plots. Other plots, which were found disturbed by grazing animals, were discarded. Examination of the undisturbed plots one year later disclosed that some 60–70% of the emerged seedlings were still alive and growing, and could, therefore, be considered as established.

DISCUSSION

Failure to germinate in the three *Convolvulus* species under investigation was clearly a result of a water-impermeable seed coat. The biological significance of such coats has been discussed elsewhere (Crocker 1906, Harrington 1916, Porter 1949, Koller 1955). Several treatments which are known to reduce coat impermeability in "hard" seeds (Barton and Crocker 1948, Porter, 1949) were effective in doing so with the three *Convolvulus* species. The inefficiency of the ethanol treatment, as compared to the impaction treatment, indicated (cf. Barton 1947) a coat structure analogous to that found in the Papilionaceae (i.e. a completely sealed coat, with a single opening which is usually plugged) rather than one analogous to that found in the Caesalpiniaceae (i.e. a coat pierced by numerous small lacunae). This indication was confirmed by anatomical studies, where the presence of the "plug" structure in an otherwise solid coat was observed. The embedding experiments proved conclusively that, as described by Hamly (1932), the impaction treatment loosens this plug, thereby permitting access of water to the embryo.

With acid treatment, a large proportion of seeds with micropylar tips embedded had nevertheless swelled. It seems that though the focal point of attack by the

* Mean annual precipitation 100 mm.

acid is the micropylar plug (as is borne out also by the anatomical evidence), other portions of the coat are also susceptible to the corrosive action of the acid, although to a lesser extent.

The question often arises whether the abrasive action of soil particles, driven at high velocity by desert winds or floods, or the high temperatures which occur on the exposed soil surface in the desert, contribute to the reduction of impermeability of the seed coat. In this connection, the failure to cause permeability with two treatments, namely sand-impaction and prolonged dry heat, is worthy of note. (It is quite likely that the relative success of the most prolonged sand-impaction is due more to impaction than to abrasion). However, it must be borne in mind that neither treatment aspires to duplicate natural conditions either in quality or in intensity. It is still open to speculation whether a different type or duration of sand abrasion, or the marked diurnal variations in soil-surface temperatures, with the resulting variation in humidity, may not be contributing factors in causing permeability in nature.

In water-permeable seeds, germination was relatively insensitive to either temperature or light. Prolonged dry storage at fairly high temperatures (26°–30°C) did not reduce this high germinability. Germination did not occur at low temperatures (5°–7°C), but no damage to the embryo resulted, and full germination occurred promptly upon raising the temperature. It would thus seem that in nature any seed which had somehow become permeable stands a good chance of germinating within the next year. If permeability is attained in summer, germinability would be maintained until the rainy season. If, however, permeability is attained in mid-winter, or the first rains occur in cold weather, the seeds would swell and remain prepared for rapid germination with the next increase in temperature. The limited experimental field reseeding tends to show that the scarce natural rainfall (100 mm per year, approximately) is sufficient for germination and establishment of a large proportion of the resulting seedlings. With reasonable planning and precautions, it seems that reseeding of ecologically similar habitats with *C. lanatus* and *C. negevensis* is quite feasible.

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RÉPARTITION EN FRANCE ET PRÉSENCE EN AUTRICHE ET EN YOUGOSLAVIE DE *DRYOPTERIS X TAVELII* ROTHM.

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ABSTRACT

Dryopteris × *tavelii* Rothm. (= *Dr. filix-mas* × *paleacea*) is new for the flora of Austria and of Yugoslavia. In France, this rare plant is scattered throughout almost the whole land.

INTRODUCTION

Dans un article qui fit progresser fortement la connaissance des *Dryopteris* du groupe de *Dr. paleacea* (Sw.) Hand-Mazz., Rothmaler (1946) définit l'hybride *Dr. filix-mas* (L.) Schott × *paleacea*; il l'appela *Dr. × tavelii* en l'honneur du ptéridologue suisse F. von Tavel. Quelques années plus tard, Reichling (1953) précisa les caractères de *Dr. × tavelii* et de ses parents, et leur distribution au Grand-Duché de Luxembourg et en Belgique. D'autres auteurs ont traité récemment de cette plante, aux points de vue floristique ou cytogénétique.

Pourtant trop de botanistes la méconnaissent encore. Une herborisation en Autriche m'a fait trouver *Dr. × tavelii* qui n'était pas encore connu de ce pays où il existe probablement ça et là. Un collègue belge a recueilli le même hybride en Yougoslavie: c'est également une acquisition nouvelle pour la floristique de ce pays. La répartition en France de la même plante est encore très imparfaitement établie; je cite les spécimens que j'ai vus de ce pays. J'ai pour ambition de faire connaître davantage cette fougère, dont l'importance au point de vue floristique ressort particulièrement bien du travail de Reichling (1954). Parmi mes herborisations, celles faites en compagnie du Professeur Michael Zohary en Belgique et dans les Alpes d'Autriche, d'Italie, de Suisse et de France, m'ont donné la joie de parler avec lui de problèmes tels que ceux abordés ici, et d'apprendre de lui beaucoup de choses. En témoignage de respectueuse gratitude, je suis heureux de lui dédier cet article.

La grande majorité des spécimens cités ci-dessous appartiennent au riche herbier de Ptéridophytes du Jardin Botanique de l'Etat (Bruxelles).

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DRYOPTERIS X TAVELII EN FRANCE

Beaucoup de floristes français méconnaissent encore *Dryopteris paleacea*, et a fortiori *Dr. x tavelii*. Pourtant, ces deux plantes sont vraisemblablement largement répandues en France. Dans le livre de vulgarisation consacré par Guilcher (1957) aux Fougères, les photos des pages 34, 36, 37, 38 et 39 se rapportent à *Dr. x tavelii* de même que certaines parties du texte; ainsi: "Les pinnules sont comme tronquées au sommet. Elles n'ont d'autres découpures que de petites dents, plus nombreuses à leur extrémité" (p. 36); et: "la membrane se flétrit (4)" (p. 39). Tout cela est malheureusement déterminé *Dr. filix-mas*.

Voici sur la répartition de *Dr. x tavelii* en France des données que des recherches ultérieures devront compléter. On peut déjà conclure que cette fougère existe vraisemblablement dans presque tout le pays. Il est probable qu'elle y pousse en maints endroits dont *Dr. paleacea* est absent, comme c'est le cas en Hollande, en Belgique, au Grand-Duché de Luxembourg, en Allemagne, en Suisse et sans doute ailleurs encore.

BASSES-PYRENEES: Ascains, cascade de Jurrutu, alt. environ 300 m, juillet 1947, B. de Retz (in Walter et Callé, Ptéridophyta Exsiccata n° 388); Bayonne, sous bois montueux de Lescourat à Saint-Etienne, octobre 1948, J. Jallu n° 129; Eaux-Bonnes, alt. 800 m, ravin frais, juillet 1953, L. Delvosalle. HAUTE-GARONNE: Cierp, mur de pierres calcaires à l'ombre, juillet 1926, Madeleine Lefebvre. ARIEGE: forêt de Sainte-Croix-Volvestre, août 1937, Ducos; forêt de Sainte-Croix, sapinière, mai 1947, Leredde. ALPES MARITIMES: Saint-Etienne-de-Tinée, Vens, août 1954, J. Callé. AVEYRON: Peyrat, ravin du Bourgnou, alt. 550 m, sol siliceux, septembre 1919, J. Soulié; vallée de la Truyère à Pons, en amont d'Entraygues, éboulis un peu ombragés, août 1939, J. Callé et E. Walter. CANTAL: Maurs, ruisseau sous Cardaillac, juillet 1946, E. Walter; Maurs, à Roquetanière, haie, L. Lavergne. AIN: signalé entre Lyon et Montluel, à La Boisse, dans un ravin boisé entaillant le rebord oriental du plateau de la Dombes, en 1953, par Chr. Bange. COTES-DU-NORD: Trévou-Tréguignec, chemin de l'étang de Boisriou et entrée du château de Boisriou, août 1935, J. Callé n° 214, 219, 222, 223, 234 et 236. MAYENNE: route de Saint-Céneri à Lachapelle-Rainsonin, octobre 1924, Ern. Rocher (déterminé *Dr. filix-mas* var. *rocheri* Lévl.). HAUTE-SAONE: route de Lure à Lantenot, fossé au bord du bois, juillet 1930, V. Madiot (Société Linnéenne de la Seine Maritime n° 941). VOSGES: Remiremont, juillet 1939, Fr. Margaine et E. Walter; Remiremont, forêt du Corroy, le long du sentier Drouat, alt. 550 m, juillet 1939, E. Walter; près de Remiremont, forêt de Sapenois, alt. 550 m, hêtraie humide sur granit, juillet 1939, E. Walter (in Walter et Callé, Pteridophyta Exsiccata n° 477). BAS-RHIN: Salm près de Rothau, alt. 600 m, sapinière-hêtraie clairière, une plante, septembre 1930, E. Walter; entre Saverne et l'Oberhof, alt. environ 300 m, sur grès vosgien, sapinière mixte, un pied isolé, septembre 1953, E. Walter. ARDENNES: Laifour, Dames-de-Meuse, rochers exposés au Nord, juin 1954, C. Vanden Berghen; Thilay, vallée de la Semois, août 1954, A. Lavalrée n° 6378; Le-Mont-Dieu, à l'est de la nationale, forêt mélangée à l'exposition nord, sur gaize marneuse oxfordienne, juin 1958, J. Duvinéaud et C. Vanden Berghen.

DRYOPTERIS X TAVELII EN AUTRICHE

WIENERWALD: entre Hochstrass et Hasenriedl, alt. environ 550 m, versant d'un petit ravin dans une hêtraie, 5 avril 1959, A. Lavalrée n° 10.346.

J'ai cueilli cette plante pendant le Symposium de Flora Europaea à Vienne, lors d'une herborisation guidée par Messieurs Erich Hübl, Hans Wagner et Gustav Wendelberger, en compagnie de Mesdames Wendelberger et Pawlowska et de Messieurs El. Landolt, B. Pawlowski et S. J. van Oostroom. Les feuilles de *Dr. x tavelii* étaient encore vertes alors que *Dr. filix-mas* ne montrait à cet endroit que feuilles sèches. Je n'ai pas vu *Dr. paleacea* dans cette localité. *Dr. x tavelii* est nouveau pour la flore d'Autriche; E. Janchen ne le cite pas dans son "Übersicht der Farne Oesterreichs" (1951) ni dans le "Conspectus Florae Austrae" de Hoefler et Knoll (1956). L. Reichling ne le connaissait pas de ce pays lorsqu'il rédigea son mémoire déjà cité (1953) et il m'a écrit (lettre du 27 avril 1959) qu'il n'avait jamais vu de spécimen autrichien de cet hybride.

DRYOPTERIS X TAVELII EN YUGOSLAVIE

SLOVENIE: Alpes Juliennes, Vrsic, à proximité de la route de Kransjska-Gora, à environ 4 km de cette dernière localité, alt. environ 1050 m, vallon boisé à l'Ouest, *Anemoneto-Fagetum*, août 1956, J. Lambinon n° 56 Y 147.

Cette fougère n'était pas connue de la Yougoslavie d'après le mémoire de Reichling (1953) déjà cité.

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REMARKS ON SOME NEW OR LITTLE KNOWN MYRMECOCHOROUS PLANTS FROM NORTH AMERICA AND EAST ASIA

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ABSTRACT

This article treats of angiosperms adapted to seed-dispersal by particular ants. In the Introduction the author gives a brief survey of mainly Swedish and Norwegian botanical literature dealing with myrmecochorous plants with special emphasis on the excellent treatise published by the Swede R. Sernander (1906). He demonstrated that European and West Asiatic myrmecochores are *derivative*, not primitive. He gives many interesting examples of myrmecochores displaying not only positive-adaptive features, but also rudimentary anatomical structures in stems and fruit-walls. Sernander was the first botanist who realised that a combined investigation of myrmecochores and their non-myrmecochorous relatives gives inquirers in reconstructive phylogeny quite new and very important aggressive means. His prophecy that myrmecochory must have existed already in Tertiary times, was affirmed in 1932 by fossil finds in North America. The present author, being a Norwegian pupil of Sernander, published in 1932-1933 four minor treatises on some unknown or little known European and Asiatic myrmecochores which he cultivated in the botanical garden in Bergen. From 1954 the Norwegian botanist R. Y. Berg has deepened the study of myrmecochores by using modern cytological and embryological methods along with experiments in nature.—The second chapter of the present article concerns some North American and East Asiatic species of the group Papaveraceae—*Chelidoniaeae* which have been cultivated by the author in Norwegian botanical gardens. The *Chelidoniaeae* comprises several monotypic genera displaying myrmecochory (*Hylomecon*, *Chelidonium*, most probably *Coreanomecon*, and *Sanguinaria*). The genus *Stylophorum*, with one North American and two East Asiatic species, seems to be entirely myrmecochorous too. The only genus belonging to the *Chelidonium*-group proper which is not myrmecochorous, is *Dicranostigma*. Besides giving descriptions of the fruits and seeds the author has tried to show that the stem-anatomy of several of the myrmecochorous species dealt with here is very peculiar and displays degenerated mechanical systems. This is especially obvious in the case of *Hylomecon*. At last the author ventilates the opinion that the traditional group *Chelidoniaeae* most probably is not a natural one as the genera *Sanguinaria*, *Eomecon*, *Macleaya*, and *Bocconia* are very different from the *Chelidonium*-group proper.

INTRODUCTION

The first European botanist who created an adequate international terminology in the important chapter of botany which to-day is called dissemination or plant

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dispersal, was Dammer (1892, 1893). At first he used the terms anemophilous, hydrophilous, and zoophilous in reference to plants whose diaspores (French: disseminules; German: Verbreitungseinheiten) are adapted to transport by wind, respectively water or animals. Later he changed the above mentioned terms to anemochorous, hydrochorous, and zoochorous. The zoochorous plants were by Sernander (1901) divided in three groups: (1) the endozoochorous plants whose diaspores are eaten by animals and mankind, but where the hard seeds or fruit-stones pass through the intestinal canal without damage; (2) the epizoochorous plants whose seeds or fruits adhere to the fleece, coat or feathers of animals, or the garments and boots of man, but gradually loosen and fall on to the ground; (3) the synzoochorous plants. The diaspores of the latter are collected systematically by animals either for making stores before the winter or the dry season comes, or for the feeding of the young.

The noun myrmecochore (Italian: mirmecocore) as applied to plants whose seeds or fruits are transported by ants, was originally used by Beguinot and Traversa (1905), but nearly simultaneously by Sernander (1906). The adjective myrmecochorous and the substantives myrmecochores (the plural) and myrmecochory have during the last 50 years been incorporated as biological (ecological) terms in nearly all the continental European languages. Sernander emphasized (1906 p. 5) that he reserved these terms to plants whose diaspores were sought out and transported by ants on account of special morphological characteristics which bear the stamp of adaptations.

Thanks to Sernander's investigations (1906) the European plants adapted to myrmecochory are fairly well known. There are, however, undoubtedly many European myrmecochorous species which still have not been recognized as such in spite of the fact that minute descriptions of the species in question are given in floras and morphological handbooks.

The present author has previously shown that for instance *Leucojum vernum*, *Narcissus triandrus*, *Colchicum autumnale* and other species of the last mentioned genus are myrmecochorous (Nordhagen 1932 a, 1933). Five years ago Berg published a treatise: "Development and dispersal of the seed of *Pedicularis silvatica* L." (Oslo 1954), which in fact is the first publication concerning myrmecochory in which the ontogeny of the diaspores is elucidated by modern anatomical and cytological methods. Berg drew the conclusion that most probably also *Pedicularis lusitanica* Hoffsg. et Link, and *P. numidica* Pomel are myrmecochores because the seeds of these species have the same extraordinary type of appendage as *P. silvatica*. Since the mother species of *P. numidica* according to Bonati (1918 p. 38) and other authors must have migrated across the Italian land bridge to North Africa towards the end of the Tertiary, the myrmecochory in this case must be old.

Sernander (1906, 1927) moreover was able to show in a conclusive way that

the study of myrmecochory within a certain plant genus or even a family gives students in reconstructive phylogeny quite new and important offensive weapons. The fact is that nearly every myrmecochorous species, when compared with its non-myrmecochorous relatives, shows obvious characters either of a positive-adaptive or of a rudimentary nature, or both. Myrmecochory is never a primitive, but always a derivative character. Sernander gave convincing examples of myrmecochores with reminiscences of anatomical structures which still have an important function among their non-myrmecochorous relatives (cp. *Hepatica triloba* p. 286-288, where the degenerate mechanical system of the stems [flower-stalks] during postfloration is described and delineated; cp. also the feeble mechanical elements in the capsule-wall of *Viola odorata* L. and other myrmecochorous species as compared with those of, for instance, the explosive *V. rupestris* F. W. Schm., delineated on p. 303).

The present author in his treatise on the Asiatic genus *Roscoeia* (Zingiberaceae), published in Bergen (1932 b), tried to show that the species can be arranged in a phylogenetic series according to the degeneration of the stem and the increase in the length of the flower tube, two phenomena which show a distinct correlation. The series is, however, incomplete and tentative as only 5 of the existing 15 *Roscoeia*-species are in cultivation in Europe, and could be studied by the author in Bergen where the winter is very mild.

Sernander showed that from an ecological point of view the majority of the European myrmecochores are forest plants; but a rather numerous group especially in the Mediterranean countries appear in our time as ruderals. The latter are usually hapaxanth, and nitrophilous. According to Sernander their original habitats seem to have been more or less open places in the Tertiary landscape where prehistoric animals had their resting- or water-places and thus created habitats fit for nitrophytes. Some of the South European myrmecochores described by Sernander and others are chasmophytes.

Sernander avoided premature conclusions as to the descent of certain myrmecochorous species or groups of species. In the final chapters "Die Organographie des fruktifikativen Systems und die postflorale Entwicklung im Vergleich zu anderen verbreitungsbio-logischen Typen" (p. 244-339) and "Entwicklungsgeschichtliche Fragen" (p. 373-394), however, he came to the conclusion that the ancestors of the present European myrmecochores probably were either ballists or plants with explosive fruits. In his treatise on *Trillium* (cp. below) Berg concludes that the existing myrmecochorous *Trillium* species most probably had endozoochorous ancestors with baccate fruits.

Sernander pointed out many genera or groups within certain genera where myrmecochory so to say has accumulated (e.g. *Melampyrum*; the section *Omphalospora* of *Veronica*; the tribe *Anchuseae* of the Boraginaceae). From own experience the present author could add the group *Galanthinae* of the Amaryllidaceae, and

Cyclamineae of the *Primulaceae* (already mentioned by Kerner 1896-1898 and Hildebrand 1898-1901, but without any description of the curious exotesta of the *Cyclamen*-seeds, which according to Nordhagen 1932 c, constitutes the attracting apparatus). As to *Viola*, the publications of J. Clausen show that the myrmecochorous species hitherto known all belong to the subgenus *Nominium*. In other families or subfamilies, sometimes even in one and the same genus, myrmecochory has established itself independently several times. In such cases myrmecochory is of polyphyletic origin. A good example is afforded by the *Fumariaceae*, where for instance *Corydalis* and in part *Dicentra* have capsules with seeds bearing an elaiosome, whereas *Fumaria capreolata* and *F. spicata* have monospermous, indehiscent fruits (nutlets) with basal elaiosome (*Hepatica*-type; Sernander 1906 p. 223-224, p. 291-295 and plate II). Within the genus *Carex* myrmecochory seems to be polyphyletic too (cp. *Carex montana* and *C. ericetorum* with *C. caryophyllaea* [= *C. verna*], or with *C. digitata* and *C. pediformis*; Sernander p. 117-122 and p. 229-230; plate III and VI); but all of them belong to the *Heterostachyae tristigmaticae*.

In the final chapters of his book Sernander summed up his vast observations and at the same time emphasised the multiplicity of the myrmecochorous plants. In spite of the fact that myrmecochory must be interpreted as a derivative quality, Sernander's opinion was that this mode of seed-dispersal must have come into existence already during the Tertiary (cp. above). An absolute proof of the correctness of this theory was later furnished by a find of fossil seeds and fruits in North America (cp. Elias: "Grasses and other Plants from the Tertiary rocks of Kansas and Colorado", 1932 p. 351, and plate XXIX figs. 2a-d). Here a nutlet of a species belonging to the *Boraginaceae*, with a well preserved elaiosome of Sernander's *Ajuga*-type, a pseudostrophiola, is pictured.

Sernander's new approach to phylogeny did not create the sensation in the botanical world which it deserved. Details from his book are, however, often quoted in ecological and sometimes in taxonomical literature, and in Hegi's *Flora von Mittel-Europa*. The present author has, as a Norwegian pupil of Sernander, tried to follow his ideas, but as yet only had the opportunity to publish some minor contributions in this field. In the latest treatise from the hands of Berg: "Seed dispersal, morphology, and phylogeny of *Trillium*" (Oslo 1958) this author has showed how vital and important the new approach to phylogeny, inaugurated by Sernander, is in modern morphology and taxonomy. Sernander never had the opportunity to travel in Asia, North Africa, and America, and this was probably the cause why he to a certain degree underrated the importance of myrmecochory outside Europe and West Asia.

Ridley (1930), after having quoted Sernander's book, gives some few examples from South Africa and South America of myrmecochory, i.e. plant-species with elaiosomes; but as he does not keep these plants apart from the "Dyzoo-

choren" (Müller 1933, 1955), Ridley's chapter "Dispersal of seeds by insects" (p. 518-527) is heterogeneous. Müller's "Dyszoochoren" are plants whose seeds are collected by quite special ants (e.g. *Messor*-species) which have strong masticatory organs. These ants prepare stores of food before the unfavourable seasons of the year, and the seeds and fruits which they have collected, are eaten. The seed-dispersal by these ants is quite accidental as only the diaspores which are lost during the transport, or stores which are forgotten, contribute to the expansion of the plant-species in question. The real myrmecochores in Sernander's meaning have an appendage to their seeds or fruits or a peculiar testa which certain ant-species bite off and use when feeding their larvae. In this case the seeds themselves are not injured. Afterwards they are carried by the ants out again from their nests and thrown away.

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When Zohary in 1937 published his treatise "Die verbreitungsökologischen Verhältnisse der Pflanzen Palästinas. I. Die antitechorischen Erscheinungen", he gave the botanical world something of a counterpart of Sernander's book. The present author was therefore very pleased when he received an invitation from the Editorial Board of the Botany Section of the Bulletin of the Research Council to participate in the issue of the "Bulletin" dedicated to Professor Zohary on his 60th birthday. The following contribution is, however, both fragmentary and in many ways preliminary.

PAPAVERACEAE — CHELIDONIEAE

Already in 1897 the American botanist Robertson published a short article about "Seed crests and myrmecophilous dissemination in certain plants". He found that the ant *Formica rufa* transported seeds of *Sanguinaria canadensis*, *Uvularia grandiflora*, and *Trillium recurvatum*, and pointed out that the seeds in question had peculiar appendages. In 1898 Kerner von Marilaun published some observations from the Botanical Garden in Vienna concerning transport by ants of the seeds of *Sanguinaria canadensis* and *Chelidonium majus*. He presumed that the appendages of the seeds lured the ants. The *Chelidonium*-mystery was, however, unravelled by Sernander (1901 p. 240; 1906 p. 49-50 and 289), the first botanist who made experiments on ant-paths. Simultaneously he discovered that the cells of seed crests and analogous appendages on diaspores transported by ants contain fatty oils. He created the name *elaiosome* for such organs.*

* Already in 1900 the Swedish botanist G. Lagerheim observed that seeds of *Viola odorata* and *V. hirta* were transported by ants, and that the appendage of these seeds contained a fatty oil. Lagerheim writes that this oil probably attracts the ants.—In Sernander's *Puschkinia*-type the whole surface of the seed has large cells containing fatty oils. In *Colchicum*-species the testa secretes sugar (Nordhagen 1933).



Figure 1

Dicranostigma franchetianum (Prain) Fedde. Indehiscent and dehiscent capsules.
Bergen, October 1936.

Both *Sanguinaria canadensis* and *Chelidonium majus* belong to the tribe *Chelidoneae* Reichb., and both are derivative as to their seed-dispersal. The most archaic or primitive genus within the tribe *Chelidoneae* is probably *Dicranostigma*, with 3 species in China-Himalaya. The author has had *D. franchetianum* (Prain) Fedde in culture both in Bergen and in Oslo. The fruits are linear, erect capsules, rather similar to those of *Chelidonium majus*; but the seeds have no crest or appendage (Figure 1). The two other species, *D. lactuoides* Hook. et Thoms. and *D. leptopodium* (Maxim.) Fedde are known to the author only from herbaria or as illustrations in handbooks (cp. Fedde 1909 fig. 25, and 1936 p. 87 fig. 42); they, too, have narrow, cylindrical, erect capsules and uncrested seeds. All of them have 2 carpels as *Chelidonium majus*; but whereas the latter has faintly explosive capsules (Sernander 1906 p. 280), opening from below by 2 turgescient and still greenish valves which separate from the placentae, the *Dicranostigma*-species seem to have non-explosive capsules, opening from the top and downwards. Also in this case the valves separate from the placentae, but gradually. According to observations on *D. franchetianum* by the author, this species belongs to the ballists of Sernander and behaves very much like Crucifers with siliquae. The stem with its branches and the fruit-stalks are not brittle, but rather stiff with a well developed sclerenchyma.

In *Dicranostigma* or rather extinct perennial *Dicranostigma*-like types one must seek the phylogenetic background for the genera *Chelidonium*, *Stylophorum*, and *Hylomecon*. All the 4 genera were united under the name *Chelidonium* by Prain (1895); he created the new name *Euchelidonium* for *C. majus*. As the crested seeds of *Chelidonium majus* and the myrmecochory of this species have been described by Sernander and others, the author is here going to deal with *Stylophorum*, *Hylomecon*, and *Sanguinaria*.

According to Fedde (1909, 1936) *Stylophorum* comprises one American species, *S. diphyllum* (Michx.) Nutt., a forest-plant in the atlantic North America, and two species in Central China, viz. *S. sutchuense* (Franch.) Fedde and *S. lasiocarpum* (Oliv.) Fedde.* The capsule in this genus has 2-4 carpels and a conspicuous crest on the raphe of the anatropous seeds. The only species which the author has had in culture in Norway is *S. diphyllum*. The morphology of this perennial species is described in many American floras, but as far as the author can see nobody has as yet discovered its beautiful adaptation to myrmecochory. The specimens which were grown in the Botanical Garden in Bergen about 1936, and which are still alive, as well as those which are now cultivated in the Botanical Garden of Oslo, are evidently selffertile (in contrast to *Hylomecon japonica*; cp. below). As seen on Figure 2 the stems of *S. diphyllum* are naked below, but have 2, less often 3,

* Fedde (1909, 1936) seems to have exchanged the picture of the capsule of *Hylomecon japonica* with that of *Stylophorum lasiocarpum*. At any rate the figure N is a capsule of *Hylomecon japonica* and not of *Stylophorum lasiocarpum*.



Figure 2

Stylophorum diphyllum (Michx.) Nutt. Parts of stems with flowers and mature, dehiscent fruits. The capsule below originally drawn 2/1.
Bergen, June 1936.



Figure 3

Dehiscent fruits of *Stylophorum diphyllum* (Michx.) Nutt. Below to the right the empty placentae, united by the shrivelled style.

subopposite apical petioled floral leaves, similar to the few long-petioled radical ones (which are not seen on the picture). Most probably this "uplift" of the large assimilating stem-leaves to the apex of the stem is an adaptation to the special light conditions in the forests where *S. diphyllum* grows. The terminal inflorescence is cymose, but umbel-like and few-flowered with 2-5 cm long erect pedicels during anthesis. The petals are yellow and 2-3 cm long. After the pollination the petals fall off, and the ripening capsules become gradually nodding. When the fruit is ripe the peduncle is either strongly curved downwards or hanging (cp. the figure).

The capsules of *S. diphyllum* have 2-4 carpels. When mature they still have a greenish colour and a cucumber-like consistence, with bristly, flattened hairs all over the surface (Figure 3). They open rather rapidly by longitudinal clefts from the apex towards the base.

The seeds fall directly from the capsule down on the forest-ground. The seed-crest, which is mentioned in many American floras, but curiously

enough not in the new Britton and Brown's "Illustrated Flora of the northeastern United States and adjacent Canada" (Vol. II, 1952), is in fact the most beautiful elaiosome that the author ever has seen. When fresh, the crest is white. It consists of 3-5 rows of long protuberances. These are outgrowths from the raphe and they give the crest as a whole a striking similarity to a tiny sea-anemone. Outside the crest the testa of the ripe seed is olive-coloured and glossy, but very soon displays a fine honeycomb-like surface due to shrivelling (Figure 3).

Experiment. In September 1959 a plant which had been potted and placed in a cold frame, produced 1 mature capsule with about 35 ripe seeds. Of these 15 were put on a patch of naked soil in a rockery with Norwegian plants, where numerous individuals of the red ant *Myrmica rubra* L. were observed. Some of the ants were transporting a bit of a root to their nest, which evidently was situated below a big specimen of *Silene cucubalus*. The locality is facing N.W. and faintly sloping. The author's watch showed 12⁴⁵. The ants immediately began to palpate the seed-crests and, seizing the seeds by the crest, ran away with them in the direction of the said *Silene*, where they went underground. After the lapse of 6 minutes all the seeds were removed. The reactions of the ants to the seed-crests were absolutely convincing. Also in Bergen in July 1936, the seeds of *S. diphyllum* were evidently taken by soil-ants as the seeds very soon disappeared from the surface of the soil; but rainy weather prevented the author from making experiments with them. The Figures 1-5 were delineated in Bergen 1936.

Under a microscope one can clearly see that each of the protuberances of the crest consists of a big terminal cell and a smaller basal one. Both contain a lot of conspicuous drops of fatty oils, which stain intense red with Sudan dye. The crest is accordingly an elaiosome in Sernander's meaning. A more detailed description of the crest and the ontogeny of it will be published in the future.

According to Gray-Fernald (1950 p. 680) *S. diphyllum* flowers from March to May (other American floras: from April to May), but its stems wither up after the dissemination in the same way as they do in many other vernal myrmecochores. A section of the hollow but strong stem, after the dissemination, shows 2 rows of lamellar collenchyma below the epidermis, and a cylinder of weakly lignified cells in the cortex, outside the vascular bundles. The latter have a cap or band of sclerenchymatic fibres in the outermost part of the phloem. The stem therefore stands erect even in September (at any rate in Oslo). It is much stronger than the stems of many other myrmecochores, and its central cavity narrower (cp. *Hylomecon* below). As the author has not had the opportunity to study *S. diphyllum* in its natural habitats and not yet had he the two Chinese species *S. sutchuense* and *S. lasiocarpum* in culture, the phylogenetic problems which the stem anatomy of *S. diphyllum* creates, can not be discussed at present. The Chinese species also have crested seeds. According to Prain (1895 p. 581-583) *S. lasiocarpum* comes nearest to the American *S. diphyllum* as its stem is leafless below but has two short-petioled apical floral leaves. *S. sutchuense*, on the other hand, has 4-7 alternate, short-petioled cauline leaves. It is highly probable that also the two Chinese species are myrmecochorous.

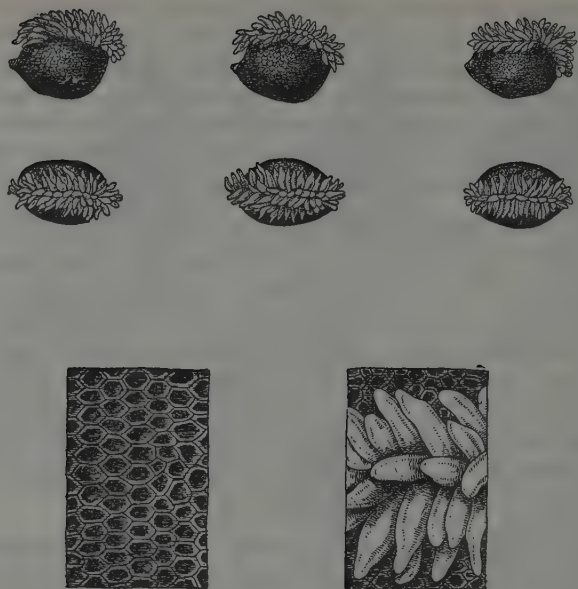


Figure 4

Above enlarged ripe seeds of *Stylophorum diphyllum* with crests.
 Below parts of the seed-surface and the crest stronger magnified.
 Bergen, June 1936.

The capsule-wall of *S. diphyllum* mainly consists of a thick parenchymatic tissue with vascular bundles; collenchyma and sclerenchyma are lacking. The fruit is succulent until dehiscence, but the valves then shrivel very soon and fall off after a few days, at any rate in Norwegian botanical gardens. Only the placentae, united by the shrivelled long style, are left, forming together a curious distorted "cage" (cp. Figure 3).

The adaptations of *S. diphyllum* to myrmecochory are easily perceptible: the seed-crest; the downwards bent peduncles and capsules, which by their way of dehiscence cause the seeds to fall directly down on the substratum immediately after maturation (tachyspory). This is very important as the seed-crests desiccate very soon when exposed to dry air, and lose their attractiveness. Similar phenomena characterize many other myrmecochores, e.g. species of *Corydalis*, *Hepatica nobilis*, *Reseda phyteuma*, species of *Nonea* (Sernander 1906) and several *Trillium* species (Berg 1958).

Hylomecon japonica (Thunb.) Prantl et Kündig (= *H. vernalis* Maxim.) is a vernal plant like *Stylophorum diphyllum*. The oldest picture of it is found in

Maximowicz: "Primitiae Florae Amurensis", published separately in 1858, but incorporated in Mém. Acad. Impér. de Sciences de St. Petersburg, Tome IX, 1859. This perennial plant has 1–3 dm high stems from a short rhizome, which also produces radical leaves with very long petioles. The stems are usually leafless below, but carry at the apex big, unequal, but always subopposite leaves, the smaller one sessile. Sometimes a small third leaf or even a fourth one is developed. The leaves are supporting 1–2 (–4) rather big yellow flowers on 3.5–7 cm long peduncles. The ovary is linear and glabrous with a long style and small erect stigmas. The bicarpellate capsules are narrowly cylindric, 2–8 cm long, tapering at the apex. The seeds according to Prain (l.c.) are small and numerous. They have a smooth shining testa, and a big crest on the raphe (cp. the immature seed depicted by Maximowicz on plate III, 5, where the crest is marked with C, and by Fedde 1909, fig. 25 Q). According to the picture published by Busch (1913) the 2 valves split from the apex of the fruit towards its base; but this is probably a mistake. Fedde (1909 p. 209) characterizes the fruit in the following way: "Siliquae bivalves valvis facile solutis —", which seems to indicate that the *Hylomecon*-fruit is rather explosive, like the fruit of *Chelidonium majus*.

The author has had *H. japonica* in culture in the Botanical Garden, Oslo (the specimens, most probably a clone, came from a Dutch nursery). The plant is evidently self sterile to a high degree. It has, however, had a few fruits, but only with very few, sometimes only one ripe seed. In 1953 the author observed that a small, blackish ant ran away with a seed which had fallen down from a mature capsule.

The seed-crest of *Hylomecon* is different from that of *Stylophorum diphyllum* in so far as its individual cells are not forming protuberances, but unite into a continuous appendage, which becomes curly when dry. The author has in his possession two samples of seeds, one from the Botanical Garden, Berlin-Dahlem, and another one from H. Correvon & Fils, Chêne-Bourgh, Switzerland. Fedde (1909 fig. 25 Q) gives an apparently correct picture of the seed, probably delineated when newly ripe. The cells of the crests of the above mentioned seeds still give a positive reaction with Sudan Red, proving that they contain fatty oils.

Hylomecon japonica, the only known species of the genus, grows in the temperate East-Asia: Amur-land, Manchuria, North China, Korea, and Japan. It keeps to deciduous forests and hazel coppices (Maximowicz 1859 p. 36). It is without doubt a myrmecochorous plant, and the author hopes to be able to give a satisfactory description of its seed-crest in the future. He has now received living plants of a self sterile strain from the Botanical Garden in Copenhagen, and by planting the Dutch and the Danish specimens together he hopes to get well-developed capsules and seeds.

The stems of *Hylomecon* are much weaker than those of *Stylophorum diphyllum*.

lum and after the dehiscence of the capsules gradually decline to the ground. In a sunny habitat in Oslo the stems disappear already in July whereas they persist until September in a shady habitat, but in half-withered condition. The stems when still erect have a big central cavity. The vascular bundles are in contrast to those of *Stylophorum diphyllum* and *Chelidonium majus* destitute of sclerenchymatic caps or bands. In the outer part of the cortex there is, however, a weak cylinder of sclerenchymatic tissue. The stem morphology of *Hylomecon japonica* comes altogether near to that of such a typical myrmecochore as *Corydalis nobilis*.

Both *Stylophorum diphyllum* and *Hylomecon japonica* behave differently from the myrmecochorous *Chelidonium majus*. The latter has strongly branched stems with tuber-like thickenings at the nodes and the base of the branches. The stem and its branches display a strong cortical sclerenchymatic cylinder, consisting of about 7-8 cell-layers. Each of the vascular bundles has a strong cap or coat of sclerenchyma, much stronger than in *Stylophorum diphyllum*.

These mechanical characteristics of *Chelidonium majus* are attributable to the strong branching of the stems and the very long flowering season of the species (in Norway from May to August). In contrast to *Chelidonium* both *Stylophorum* and *Hylomecon* only have one inflorescence, at the apex of the stem, and their flowering season is a short one.

Of these 3 myrmecochorous genera *Hylomecon* has the weakest stem, i.e. the most degenerate mechanical system.

∴

The author has never seen the interesting monotypic genus *Coreanomecon* Nakai, with *C. hylomeconoides* Nakai. According to Fedde (1936 p. 65) the seeds are crested. This is a plant of shady woods in South Korea, and in all probability it is myrmecochorous. Unfortunately, the author has as yet not found full description neither of the capsules nor of the seeds.

∴

The myrmecochory of the beautiful, white-flowered *Sanguinaria canadensis* L. was, as stated above, detected by Robertson (1897). He had in fact made his observations already in 1889, and they are mentioned by Trelease in a treatise on myrmecophilism in the periodical "Psyche" (tome 179, 1889). In 1942 Gates published an article "The dissemination by ants of the seeds of Bloodroot, *Sanguinaria canadensis*" in "Rhodora". Curiously enough Gates does not quote the paper of Robertson. Gates found that 12 different species of ants made prompt positive reactions, usually dragging the fresh seeds away by the crest. But he does not discuss the morphology of the plant, nor the anatomy of the seed-crest. Gates presumed that the crest contains oil and is a real elaiosome.

The author had *S. canadensis* in culture in the Botanical Garden in Bergen about 35 years ago. The plants were imported from Holland and flowered freely

3 or 4 years after having been planted in a rock-garden. They perished during a hard winter. The species is obviously self fertile as the 1-locular, 2-valved capsules were beautifully developed in Bergen. Usually they ripened in the last weeks of June, and they were greenish, somewhat inflated, and faintly explosive when mature. The 2 valves split rather rapidly from the base towards the apex when touched, and the seeds fell to the ground. Only the placentae, which were united by the style, were left on top of the scape; but already in July the latter withered and disappeared (in Bergen). Each rhizome produces one single, large long-petioled palmate leaf, which is 10–20 cm broad, with a crenate margin (cp. Figure 5). In Bergen the leaves usually overtopped the ripe capsules. The seeds are light brown with a smooth and shining testa and a very conspicuous white crest. The crest seems to be an outgrowth of the raphe, perhaps in part also of the chalaza. The micropyle is visible without a lens; it looks like a dark spot, and the seed itself is often faintly drawn out like a small spout in the micropyle region (cp. Figure 4). The cells of the hyaline crest are very large (up to 100 μ broad and 500–800 μ long), sack-like and thin-walled. They are rich in plasma, without starch-grains, and show traces of fatty oils.

The capsule-wall has below the epidermis a parenchymatic tissue with chlorophyll, and in this tissue the laticifers and the vascular bundles are imbedded. The bundles seem to have no cap or band of sclerenchymatic cells. Inward, against the cavity of the capsule, there is a curious, sharply circumscribed epidermal layer of roundish or ellipsoidic empty cells, with porous and reticulately thickened walls. These cells of the inner epidermis arch into the cavity like roundish papillae. In the mature capsule, especially the parenchymatic cells which lie on the outer side of the above mentioned curious layer, are very rich in starch-grains.

Kraus (1866 p. 118–121) has described a similar inner epidermis from the fruit-wall of *Chelidonium majus*. Its function is so far unknown.

The stem* or fruit-stalk has no ribs. Below its epidermis follow two cell-layers, the outer collenchymatous. Then comes an undifferentiated homogeneous parenchyma filled up with large starch grains. In this parenchyma the 7–8 vascular bundles are imbedded. The bundles have on their outer side a strong band or cap of sclerenchymatic cells, but a perivascular cylinder of sclerenchyma is lacking. The bundles are hadrocentric because there is phloem both inside the xylem and on both sides of it. The thickest phloem, however, is situated on the outside of the xylem. Already Möbius (1887, p. 12) showed that *Papaver umbrosum* has hadrocentric bundles in an exterior ring of bundles, and some leptocentric ones nearer the middle of the stem, so the bundles of *Sanguinaria cana-*

* According to Murbeck (1912–13, p. 66) it is not yet settled whether the single flower with its stalk is axillary to the first leaf, or terminal; but Murbeck comes to the conclusion that the latter alternative is the most probable one and has drawn the flower diagram in conformity with this.

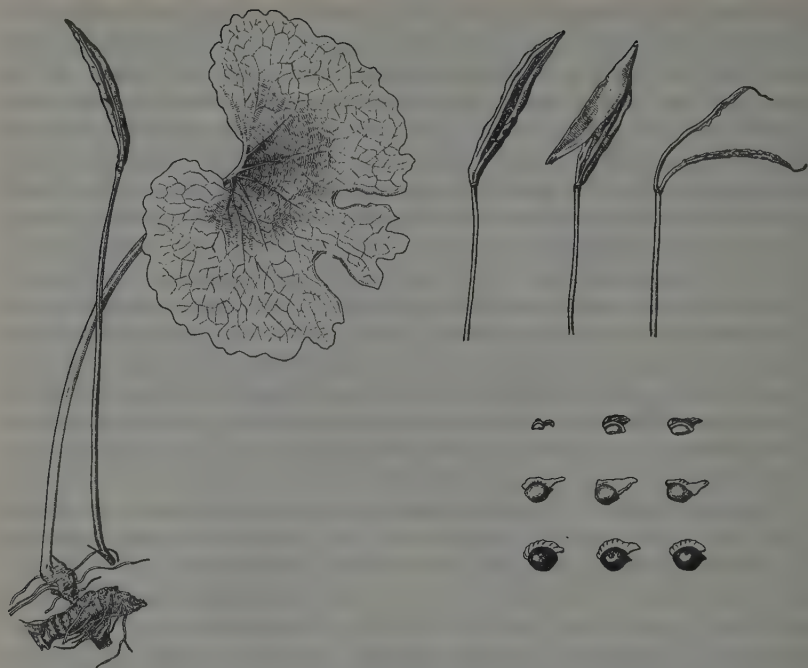


Figure 5

Sanguinaria canadensis L. To the left a mature capsule and a leaf, to the right dehiscent capsules, and seeds with crest, both immature and mature.

Bergen, June 1936.

densis are not unique within the Papaveraceae. Very striking is the richness in starch-grains of the parenchyma of the stalk, present as late as at the dehiscence of the capsule.

In comparison with many other Papaveraceae, the stem (fruit-stalk) of *Sanguinaria* is structurally weak because no special sclerenchyma is developed in the cortex outside the vascular strands.

In Bergen the fruit-stalks very often were more or less bent under the weight of the relatively heavy fruit. Robertson (1897 p. 288) writes the following about the fruits: "In *Sanguinaria* the follicles remain erect or fall over upon the ground". The present author has never seen the capsules in the latter position; but in botanical gardens the specimens usually grow in clusters, and as they have big and rather stiff leaves, the capsules usually lean upon them.

Sanguinaria canadensis is without doubt a very old species, firstly because the genus is monotypic, and secondly because the species never has been found out-

side the atlantic North America. The opinion of Fedde (1909, 1936) seems to have been that the nearest relative to *Sanguinaria* must be sought in the Chinese *Eomecon chionantha* Hance. Also this genus is monotypic, and like *Sanguinaria* it has white flowers, and leafless stems, but these are subpaniculately branched above with 6-8, perhaps more, flowers. The leaves of *Eomecon* are long-petioled, broadly cordiform with a very deep, closed or open, sinus and a broadly sinuate margin. In contrast to *Sanguinaria* which has 2+3-8 petals (Murbeck 1912-13 p. 68-69) and 20-40 stamens (Murbeck p. 71 ff.), *Eomecon* only has 4 petals, but 70 or more stamens. Unfortunately the fruit and the seeds of *Eomecon* are practically unknown. The author once purchased some specimens from a nurseryman near London, and tried artificial pollination in a cold greenhouse in Bergen; but the specimens evidently belonged to one and the same clone, and they were self sterile.

At any rate *Sanguinaria* and *Eomecon* show a greater accordance mutually than with the *Dicranostigma* — *Chelidonium* — *Stylophorum* — *Hylomecon* — *Coreanomecon*-group. According to Darlington and Wylie (1955) the last mentioned group seems to have the diploid chromosome number 12 (as to *Dicranostigma franchetianum* the number is probably not finally settled as both 12 and 16 are given in publications quoted by the said authors). Whether or not *Eomecon* like *Sanguinaria* is myrmecochorous is still an open question. In many ways *Eomecon* conveys the impression of being a more primitive genus than *Sanguinaria*; but all reflections concerning an eventual phylogenetic interdependence between the Chinese *Eomecon* and the North American *Sanguinaria* must pro tempore be considered fruitless especially because our knowledge of the morphology of the capsule and seeds, not to speak of *Eomecon*'s mode of dispersal, are practically nil.

As the chromosome numbers of these two genera seem to be unknown, it is also impossible to make a comparison with the rest of the *Chelidonieae*, viz. the East Asian genus *Macleaya* and the Central and South American genus *Bocconia*. According to Darlington and Wylie *Macleaya cordata* has the diploid number 20, which is also the case with *Bocconia frutescens*. According to Hutchinson (1920 p. 276) *Macleaya cordata* has crested seeds; but its lateral crest is narrow, and the author has not had the opportunity to study it because the species hardly ripens its fruits and seeds in Norwegian gardens. In Middle European gardens the author has seen ripe capsules. They had 2-6 seeds which were relatively firmly fastened to the placentae. When mature, the two flattened valves slip from each other like the two blades in a pair of scissors, forming a sort of samara. Probably these diaspores are anemochorous; but one ought to investigate whether or not the seeds afterwards are dispersed by ants (cp. the curious capsules of certain *Polygala* species, which are dispersed by wind, but where the seeds later on are transported by ants; Sernander 1906 p. 232-233).

The genus *Bocconia* has according to Hutchinson (1920) fruits with 2 fleshy valves and a single large seed, which at the base is surrounded by a cupular, wrinkled aril. In some species this aril is coloured (in *B. pearcei* Hutch. it is red). The mode of dispersal seems to be unknown (birds?).

According to the author's opinion the group *Chelidoniae* probably is not a natural one. The leaves of *Sanguinaria* are very different from those of the *Chelidonium* group, but have a certain likeness to a *Macleaya* leaf, which, however, shows a much more complicated configuration. Both *Macleaya* and *Bocconia* are according to Murbeck (op. cit.) derivative as to their flowers which are apetalous. The opinion of Murbeck was that the original petals of these flowers are not aborted, but transformed into stamens. These problems are, however, too complex to be discussed here.

The group *Chelidoniae*, whether natural or not, is extremely interesting since the only genus which seems to have a primitive fruit and seeds without a crest or an aril, is *Dicranostigma*. As we have seen, several of the genera are monotypic or show wide geographic disjunction in modern times (cp. the *Stylophorum* species).

The monotypic genera have to-day a restricted distribution with the exception of *Chelidonium*, which has become something of a cosmopolitan weed. It might very well be reckoned to the ruderal-group of Sernander. It is otherwise very interesting to ascertain how many of the above described myrmecochores are forest-plants (cp. the introduction to this article).

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THE ORIGIN OF THE EGYPTIAN CLOVER WITH CRITICAL REVISION OF SOME CLOSELY RELATED SPECIES

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ABSTRACT

While the origin of the Egyptian clover is still debated, Aaronsohn (1910) and Eig (1934) asserted that it grows wild in Palestine. Lack of clear definition and knowledge of the wild species related to *Trifolium alexandrinum* and of the variability of the cultivated species have frustrated previous efforts to settle the question definitely.

T. berytheum Boiss. et Blanche sensu lato, known from the coastal plain of the Lebanon, is shown to grow wild also behind the dunes of the Mediterranean Sea from the Lebanese boundary to the Philistaeon Plain in Israel. It is a variety of *T. alexandrinum*, doubtfully distinguished from the Linnaean type species. Both vary considerably in their distinctive characters, forming a complex with intermediate properties.

Claims in favour of *T. panormitanum*, *leucanthum*, *apertum*, etc. are invalidated. *T. carmeli* Boiss. and *T. vavilovi* Eig, insufficiently defined by their authors, are described anew in detail. They are similar to *T. alexandrinum*, but less so than *T. berytheum*, which must be regarded as the main genetical source from which man developed *T. alexandrinum* by selection. Its ecological adaptation to heavy inundated soils strengthens this conclusion, first expressed by Trabut (1910) without evidence. Little studied wild races of *T. alexandrinum* seem to exist in the Upper Jordan Valley. They may also have contributed their share to the origin of the Egyptian clover.

While there is no reason to look for an extinct ancestor of this clover, its origin has been quite analogous to that of other clovers which are known to occur both as wild and cultivated races close to each other.

INTRODUCTION

The origin of the "berseem", Egyptian or Alexandrian clover (*Trifolium alexandrinum* L.) is one of the long-debated riddles in the history of cultivated plants. It has not been found wild in Egypt. Models or drawings by the ancient Egyptians have not been found, nor have seeds been found in the tombs of the Pharaohs, a fact emphasized by Schweinfurth (cited after Fairchild).

Earlier authors have expressed the opinion that it was introduced into Egypt from Anterior Asia. Delile (1824) stated that in his days seeds were frequently imported into Egypt from Syria, "where this clover is cultivated and possibly grows wild". Boissier wrote in his "Diagnoses" (1856): "Cum *Trifolium alexan-*

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drinum spontaneum ignotum sit, et in Aegypto nonnisi cultum occurrat, lubenter suspicarer *Tr. constantinopolitanum* eius typum spontaneum esse". *T. constantinopolitanum* Ser., a narrow-throated species, distinguished from Linné's *T. alexandrinum* also by glabrescent or short-pubescent calyces with narrow, awl-shaped teeth, grows wild in Turkey, Syria and the Lebanon, i.e. to the north-east of Egypt, but apparently is missing in Palestine, though it was reported by Bornmueller from Jaffa (1914) and by himself (1912) and Dinsmore (in Post and Dinsmore 1932) from Tabigha on the shore of the Sea of Galilee.

An origin still further to the north is assumed by Bobrov (1945), who described a new clover of his Section *Hiantia* of subgenus *Lagopus* from the north-western slopes of the Caucasus, under the name of *T. apertum* Bobr. He finds it so similar to the cultivated berseem of Egypt that it might be regarded as its ancestor. Since this species was found also on the Black Sea shore and further to the south, in Turkey, this would strengthen the hypothesis reported by Hegi (1923) and Becker-Dillingen (1922) on the authority of Reynier, that the Mameluks who came from the Caucasus (Georgia) introduced the "Egyptian" clover into Egypt in about the 12th century of our era.

Thus, while there seems to exist a far-reaching agreement regarding the origin of the Egyptian clover in Anterior Asia * whence also other cultivated crops, like wheat, reached Egypt, it seems more natural to look for the wild progenitor or nearest contemporaneous relative in the immediate neighbourhood of Egypt, rather than in distant countries. Our attention is thus drawn to Palestine, where the presence of *T. alexandrinum* L. had already been reported by Hasselquist (1756), though like many authors after him, he did not state whether the plant found by him was wild or cultivated.

The assertion of its occurrence as a wild species in Palestine was first made by Aaronsohn (1910), who wrote: "There are also good reasons for believing that berseem (*T. alexandrinum*) originated in Palestine, though we do not know definitely where it was first cultivated. But it grows wild there, as does also *T. carmeli*, from which it differs only in slight botanical characters. ** Moreover, *T. panormitanum* and *T. supinum*, very closely related to *T. alexandrinum*, grow wild in Palestine. The fact that this whole group of closely related species grows wild in this region seems to indicate that they originated here". Aaronsohn added that Egyptian clover was not cultivated much by the natives of Palestine, the spe-

* Becker-Dillingen (1922), however, mentioned a rather vague and uncontrolled report, according to which the berseem was brought to Egypt from the Balkan Peninsula during the 6th century of our era.

** Zemach (1931) assumed that Aaronsohn expressed his opinion only on the authority of Boissier. This is wrong, since, as will be shown, Aaronsohn had collected in Palestine both wild and cultivated *alexandrinum* clover, as well as numerous specimens of *T. carmeli*, though he, as many other botanists, possibly did not arrive at a clear distinction between the two species.

cies being mainly "sown with barley in the autumn along the coast, where the rainfall is as low as 14 to 16 inches per annum". These notes imply that Aaronsohn knew of the cultivation of berseem by indigenous farmers in Palestine instead of by European colonists, mainly in the region of Gaza, where the rainfall corresponds to his indications. This centre of cultivation, however, might be interpreted not only as a primary, but also as a secondary one, arising in not-too-distant past under Egyptian influence.

Aaronsohn's opinion was also accepted by Eig (cf. Zemach 1931). Eig (1934) points out that he had in the Herbarium of the Hebrew University a wild clover which comes very near to the Lebanese *T. berytheum*. He calls it *T. judaicum* ad interim. *T. berytheum* Boiss. et Blanche was united with *T. alexandrinum* as one of its wild growing varieties by Trabut (1910), and later on by Thiébaud (1936, 1940). Eig's insufficiently described *T. judaicum* could, therefore, be included in the range of *T. alexandrinum* L. as one of its wild growing types. Eig, however, preferred to attach it to *T. berytheum*, which he considered a species very closely related to *T. alexandrinum*, but to be kept separate. Eig, like Aaronsohn, died before he had been able to study the matter further.

The idea that *T. berytheum* is the wild form of the Egyptian clover was first clearly pronounced by the great French botanist, L. Trabut, who has introduced Egyptian clover into general use in Algeria. In a paper published in 1910, he says quite definitely, on p. 2: "D'un autre côté, le *T. berytheum* Boiss. Diagnoses (*T. supinum* var. β *tuberculatum* Boiss. Flora Orientalis) doit être rattaché comme variété au *T. alexandrinum*; il représente probablement la forme sauvage".

To settle the complicated problem of the origin of the Egyptian clover conclusively, a detailed critical investigation of the whole group of "open-mouthed" *Lagopus* clovers of the Near East was advocated by Bornmueller (1914), and particularly by Eig (1934), who wrote: "We consider an investigation of the polymorphism of *T. alexandrinum* as indispensable, especially in Syria and Palestine, as well as a detailed study of the wild growing representatives of the *Maritima*-group in these countries, especially *T. berytheum* and *vavilovi*". The present investigation is a step in this direction.

NEW INVESTIGATIONS

Initial Difficulties

Difficulties of classification in the series *Aperta* which virtually coincides with the *alexandrinum*-complex, arise mainly from the insufficient description of the species in the standard works, like Boissier's "Flora Orientalis" (1872) and Post's "Flora of Syria, Palestine and Sinai" (1932). The matter is further complicated by the description of some new species by Eig (1934), Bobrov (1945), and Mouterde (1953), since the characteristics distinguishing them from closely related species described earlier are not easy to grasp.

Progress was achieved only when we were able to consult original material of *T. alexandrinum* in Linné's Herbarium in London, as well as the type material of *T. berytheum* from Boissier's Herbarium (Geneva), by courtesy of Professor Ch. Baehni. Also, Russian publications on *T. apertum* by Dr. Bobrov and others, kindly presented to us on a visit to the Herbarium of the Botanical Institute of the Academy of Science in Leningrad, proved extremely helpful.

Wild "*alexandrinum*"

In the Kishon plain, north-east of Haifa, we were surprised to find, in 1954, on heavy and wet alluvial soil a white-blooming clover reaching the height of about 60 to 80 cm. It looked as if it were the wild *alexandrinum*, being distinguished *prima vista* by its white, shining silky calyces and the apparently darker and more densely pubescent leaves. It grew on land a little higher above the water level than *T. resupinatum* var. *suaveolens* (Willd.) Dinsm., which was found nearby in drainage ditches. The wild *T. alexandrinum* proved extremely frequent in the neighbourhood on recently drained and cultivated swampy stretches.

Doubts based on its possible escape from cultivation could be refuted when we also found it under similar edaphic conditions near the new Central Railway Station in Tel Aviv, where it formed a component of a natural vegetation cover. Among its companion species we noted: *Agrostis verticillata*, *Hordeum marinum* forming large patches, *Juncus tenageia*, *Ranunculus trachycarpus*, *Plantago lanceolata* var. *altissima*, *Melilotus* sp., and *Medicago ciliaris*, all characteristic of wet, heavy soils, as well as *T. petrisavii* and *T. spumosum*.

Further south, we collected it on wet alluvial soil near Nabi Rubin (about 15 km south of Jaffa), together with the just mentioned species of *Plantago* and *Trifolium*, and in addition *Phalaris paradoxa*, *T. resupinatum* var. *suaveolens*, *Lactuca saligna*, *Bromus brachystachys*, *Pulicaria dysenterica*, etc. It disappeared where the hydrophyte *Panicum repens* became dominant as well as on drier places where one meets with *T. campestre*, *Plantago lagopus*, or *Medicago hispida*, preferring tracts about 30 to 100 cm above the spring water level. Still further south, we found the plant extremely widespread on heavy soil, which is usually inundated in winter between Gealyah, to the north of Yavneh, and the River Sukrer near Ashdod. In the north, near the Lebanese boundary, we collected it at Nahariya, not far from the seashore.

We assume, therefore, that it exists along the whole sea coast of Israel and Lebanon, from the Gaza Strip to Tripoli. It grows under conditions of cultivation and drainage only in the initial stages, and is smothered quickly by rank annuals, like *Avena sterilis*, *Ammi visnaga*, *Scolymus maculatus*, *Ridolfia segetum*, *Cichorium pumilum*, and *Centaurea verutum*, or by perennials dominating after recurring cultivation, like *Sorghum halepense*, *Cynodon dactylon* or *Convolvulus betonicifolius*. It also was found growing profusely near the edge of drainage ditches of roads and on the slopes of wadi beds.

We suppose that the clover collected by us east of Jaffa is identical with "*T. constantinopolitanum*" collected here by Bornmueller (1912). It was further found on the new campus of the Hebrew University in Jerusalem (cf. Rechinger 1952), possibly adventitiously, and together with berseem escaped from cultivation.

After closer examination and comparison with Lebanese material, we are now convinced that our plant is identical with *T. berytheum* Boiss. et Bl. However, it differs slightly from Boissier's description in the "Diagnoses" mainly by its heads, which are often borne on peduncles reaching a maximum length of 7 cm. They are thus often, but not always, sessile, as in the case of the type material collected by Blanche in the coastal region of the Lebanon. At maturity, the throat of their calyces is closed by hirsute hairs, while a callous ring is lacking or little developed, a feature justifying classification within the *Hiantia* or *Aperta* group.

Blanche collected his plants near Saida (Sidon) in the estuary of the coastal river Sainib, in a grain field. The ecological conditions of the occurrence in Lebanese territory are thus evidently the same as those found on the Israel side of the frontier. Similar edaphic conditions were indicated also by Eig for his *T. judaicum* which, as we recently could corroborate, is identical with our material.

Revision of the Species Closely Related to the Egyptian Clover

Morphological and ecological affinities thus strongly suggested a derivation of the berseem from *T. berytheum*. However, it appeared imperative to examine also other nearly related species, which alternatively might be or have actually been considered as its species of origin.

Claims for *T. echinatum* M.B. (*T. supinum* Savi) and *T. panormitanum* mentioned by Aaronsohn (1910) can be rejected from the outset, though both occur in Palestine, and the latter, under the name of *T. squarrosus* L. has recently been quoted as the prototype of the fahl variety of berseem by Sachs (1957). Both species—in addition to other differences—have calyces closed by callosities and are, therefore, less closely related to the berseem than similar, but open-mouthed species. The same holds true for *T. leucanthum* M.B. occurring in Upper Galilee.

Our attention was, therefore, attracted chiefly to *T. carmeli* Boiss. and *T. vavilovi* Eig, both endemic in Palestine and Syria and obviously related rather closely to *T. alexandrinum*. Further also *T. constantinopolitanum* had to be considered, as well as its doubtful variety *plumosum* Bornm., which is possibly identical with *T. berytheum*. Also, *T. phleodeum* Thiéb. (*T. alexandrinum* var. *phleoides*) needed examination (though Mouterde found it difficult to separate it from *T. constantinopolitanum*). The same is true of *T. apertum* Bobr. Other species, such as Post's *T. plebeium* and *alsadami* and Mouterde's *T. bonnevilliei* and *salmoneum*, are relatively rare, and less similar to the berseem than at least part of the aforementioned species.

Unfortunately, most of these binomials are rather ill-defined. Of *T. carmeli* we possess a relatively detailed description by Boissier. However, it is not sufficient

for a clear distinction from *T. vavilovi* Eig, and also not correct in every detail. *T. vavilovi* has been described by its author in a rather negligent manner. It seems that the description was founded on scarce material. *T. constantinopolitanum* was described quite insufficiently by Seringe in a manuscript and published by De Candolle in his "Prodromus" (1825).

The type material collected by L. Castagne in 1822 is kept in De Candolle's herbarium at Geneva. As we concluded recently, it appears to be *T. alexandrinum*, but differs by an urceolate calyx constricted above, bearing spreading dense, short and stiff hairs. But what seems more important, it has a closed calyx throat and must, therefore, be considered as closely related to *T. echinatum* (*T. supinum* Savi) instead of to *T. alexandrinum*. This had already been recognized by Gibelli and Belli who in Boissier's Herbarium attached a note to a sheet with material of *T. constantinopolitanum* collected by Balansa on the Kilsali Island near Ismir and determined by Boissier as *T. alexandrinum* L. var. *phleoides* Boiss. They state definitely that this ill-described species has nothing to do with *T. alexandrinum*, in spite of the resemblance of its vegetative characters. It should be considered as an independent species or subspecies. Accordingly, Hermann (1935-36) drew it to *T. echinatum* as a subspecies. We further stated that already Blanche had disproved Boissier's above hypothesis regarding the origin of *T. alexandrinum* (Herb. Boiss. in Scheda, No. 130). As he points out, he had found at Tripoli (Lebanon), wild *T. alexandrinum* distinct from *T. constantinopolitanum* occurring there also.

Later authors, as Bornmüller and Samuelsson, erroneously determined as *T. constantinopolitanum* either *T. vavilovi* or *berylbeum*. The former's var. *plumosum* is evidently none other than *T. berylbeum*.

Following the revision of recently collected material in the Herbarium of the Department of Botany, The Hebrew University of Jerusalem, as well as of specimens collected by Aaronsohn in the beginning of the present century, we publish here new, detailed descriptions of both *T. carmeli* and *T. vavilovi*.

Trifolium carmeli Boiss. Diagnoses Ser. 2, 2: 16 (1856); Fl. or. 2: 127 (1872) emend. Opphr. (Figures 1, 2, 7).

Annuum, ramosum, patule pubescens, radice subfusiformi descendente, caule erecto \pm fistuloso iam inferne et saepe a basi ramoso, 25-35 (rarius usque ad 75) cm alto, 1-3 mm lato. Rami \pm flexuosi, indistincte et tenuiter costati-sulcati, iterumque ad 60° dichotome ramosi. *Stipulae* membranaceae, oblongae aut abbreviatae, viridi-aut nigro-striatae, ciliatae, in caudas teneras plumosas striatas, eis breviores, aequilongas aut longiores abeuntes (*stipulae* foliorum superiorum dilatatae caudis petiola aequantibus); *folia* fere alterna, sed summa opposita, inferiora longe (ad 7.5 cm), superiora breviter petiolata; *foliola* tenera, \pm patule pubescentia, ca. 1-4 cm longa et usque ad 2.2 cm lata, obovata aut superne rhomboideo-lanceolata, apicem versus obsolete denticulata et saepe retusa et/aut mucronulata. *Capitula* pseudo-apicalia et axillaria pedunculis breviter hirsutis gracilibus, 0.6-1 mm latis et usque ad 5 cm longis suffulta, densissime congesta, 1-2 cm longa et

lata, ad basin ob dentes calycinos longiusculos subpungentia-echinata, fructifera ovato-globulosa aut elliptica, echinata, 1.2–1.8 cm longa. *Flosculi* albidii, in statu sicco ochroleuci, 11–15 mm longi; *calyx* brevissimus, 1.5–2 mm longus, oblongo-conicus, costis latiusculis validis decemcostatus, 5–(rarissime 4–) dentatus, praesertim superne pilis albidis patulis hispidissimus, dentibus e basi triangulari longe et anguste linearibus-subulatis, 0–1–nerviis, sub apice saepius albidis, summo apice purpureis, superioribus tubo subaequilongis, lateralibus subduplo, inferiore – ca 5 mm longo – subtriplo longiore, faux glabriuscula nitida alba, late aperta post anthesin propter disiunctionem epidermaticam callosa angustata; *vexillum* basi longiuscule tubuloso-stipitatum, anguste triangulare, apice ± elongato-caudato obtusiusculo; *alae* suboblique ellipticae-oblongae, basi auriculatae, apice acutiusculae sive obtusae *carinam* late ovatam, purpureo-maculatam, paulo sed distincte superantes. *Legumen* turbinatum, membranaceum, brunnescens, operculo scutellato brunneo tectum. *Semina* parvula, badio-lutea, subcompressa ovato-triangularia, ad hilum subretusa (Boiss.) aut potius subglobosa.*

Remark: The author saw in the Kew Herbarium, co-type-specimens collected by Boissier on Mt. Carmel in 1846.

Hab. Ca**: 1846, E. Boissier (co-type, Kew Herbarium); env. of Khirbet Loubiya, 31.3.1916, A. Aaronsohn (AH 5135); Zikhron Yaaqov 1903, 1907, etc. A. Aaronsohn (AH 5096, 5008, 5063) both localities cited by M. Evenari (1941) for *T. alexandrinum*; below Mukhraka, among the Cenomanian rocks, on the eastern slope of Mt. Carmel, 1.4.1916, A. Aaronsohn. A doubtful specimen reminding *T. vavilovi* by much shortened upper and lateral calyx teeth. From HUJ: Ca: Wadi Shaanan, 5.5.1927, N. Naftolsky; Yagur, 26.3.1931, N. Naftolsky; Yaarot Hacarmel, in *Pinetum halepensis*, 15.4.1955, N. Feinbrun; Shefeya to Bat Shelomo, 16.4.1955, A. Grizi. Sh: Tel Tsur, 26.3.1956, M. Zohary. UG: Wadi betw. Khirbet Sartaba and Jermak, in *Quercus calliprinos* and *Qu. infectoria* stands, 10.4.1951, N. Feinbrun. J: Jerusalem, courtyard, 10.4.1952, N. Feinbrun (flowering).

Trifolium vavilovi Eig in Bull. appl. Bot. Genet. Pl. Breed., Ser. 7, No. 1:108 (1934) emend. Opphr. (Figures 3, 6).

Annuum, radice teretiuscula descendente ramosa. Caulis erectus, 10–30 cm altus, saepius a basi, rarius superne solum ramosus, dichotome hinc inde inflexus, ramis costatis ramulos floriferos edentibus; inferioribus validis ascendentibus, ut caules patule pubescentibus. *Stipulae* oblongae, superne abbreviatae, membranaceae, hirsuto-ciliatae, in caudas tenues, viridi-, purpureo- aut nigro-striatas, aequilongas aut – ad folia superiora – longiores abeuntes; *folia* alterna, summa autem opposita, sparsa, saepius parvius-

- Annual, with spreading-pubescent hair, branching from below, 25–35 cm high, with indistinctly sulcate branches. Stipules membranaceous, the basal about as long as the free portion; leaves alternate except the uppermost pair, the lower long-, the upper short-petioled, ovate to rhombic-lanceolate, retuse or mucronulate and denticulate. Heads pseudo-apical and axillary, ovate-spherical, peduncled, very compact, 1–2 cm long and broad, with white florets, soon becoming echinate by spinescent calyx-teeth. Calyx tube oblong-conical, 1.5–2 mm long, 10-nerved with five subulate long-hispid teeth, the upper as long as tube, the lower nearly three times longer; throat glabrescent, open, but narrowed at maturity by epidermal callosities; standard narrowly triangular, long stipitate, elongated, wings longer than purple-tipped keel. Legume turbate, membranaceous. Seeds small, reddish-brown or yellow.

- ABBREVIATIONS: *Districts*: AP-Acre Plain; Ca-Carmel; EP-Esdrælon Plain; J-Judean Mountains; LG-Lower Galilee; Sh-Sharon Plain; UG-Upper Galilee; UJ-Upper Jordan Valley. *Herbaria*: AH-Aaronsohn Herbarium, Zikhron Yaaqov; HUJ-Hebrew University Herbarium, Jerusalem.

cula, inferiora longe (ad 5 cm), superiora breviter (4–10 mm) petiolata, \pm patule pubescentia aut hirsuta pilis albidis aut lutescentibus, aliis — praecipue illis ad nervos et margines insertis — ex tuberculo parvulo ortis, aliis ab initio cylindricis; *foliola* secundum locum insertionis inferne obovata aut elliptica, superne rhomboideo-lanceolata nec non linearia, apicem versus obsolete denticulata, 0.5–2.8 cm longa. *Capitula* pseudo-terminalia et axillaria, parvula, 7–17 mm longa, ovata aut obovato-obconica, \pm longe (usque ad 5 cm) pedunculata, *flosculis* albidis, post anthesin lutescentibus, laxiuscule subverticillatim dispositis composita, pendunculo adpressiuscule pubescente aut hirtio suffulta; fructifera elongata, ovato-conica aut oblonga, propter dentes calycinis rigidulos subechinata. *Calyx* oblongus, deinde campanulatus, ca. 2 mm longus, inferne distinctissime, sub dentibus indistincte 10-costatus, 5– (rarius 6–7) dentatus, fauce glabrescens, ad basin \pm hirtus, superne hirsutus, dentibus lanceolato-linearibus, \pm distincte uninerviis et valde inaequalibus, longitudine variabilibus, inferiore ceteris saepe latiore, tubo subduplo (usque ad duplum et dimidium secundum Eigium) longiore, lateralibus tubo aequilongis, superioribus eo paulum aut subdimidio brevioribus, omnibus pilis ex tuberculo ortis plumose hirtis aut hirsutis, sub apice subulatis albidis, ipso apice purpureis; fructiferus dimidio maior, fauce non callosa et sparse ciliatula, late aperta, dentibus inferioribus praecipue flosculorum inferiorum extus et deorsum arcuatis; *vexillum* latiusculum oblongum, 8–12 mm longum, ad basin 3 mm latum, apice rotundato et retuso, erosulo, ad basin sinuato-auriculatum et latiuscule tubulato-stipitatum; *alae* obovato-oblongae, obtusae, 4 mm longae, 1.5 mm latae, ad basin auriculo-obovato-acuminato praeditae, carinam paulum superantes; *carina* ovato-oblonga, ad basin obtusata nec auriculata; tubus staminalis (incl. stameras) 7 mm longus; stigma breviter cristatum. *Legumen* pyxidato-obovatum, membranaceum, operculo validiore subhemispherico tectum. *Semen* badio-purpureum sive viridi-luteum, ovato-acuminatum, ad hilum retusum, 1.5–1.8 mm longum et usque ad 0.8 mm latum.*

Type specimen not seen.

Hab. Ca: Mt. Carmel, 10.4.1926, N. Naftolsky. UG: Mt. Canaan, 6.5.1955, Y. Waisel; Kerem Ben-Zimra, fallow field, 12.5.1956, M. Feldman; Alma to Dishon, on terra rossa, 12.5.1956, A. Grizi; Baream, 6.5.1955, Y. Waisel. LG: Neveh Ya'ar, 11.4.1955, H. R. Oppenheimer (AH); Mahnayim, in field of vetches, 13.4.1956, T. Segall. EP: Balfouria, fields, 12.6.1925, N. Naftolsky; Kfar Yehezkiel, 26.4.1926, N. Naftolsky; south of Affule, 19.5.1953, M. Zohary; Tserifin to Affule, 13.5.1927, N. Naftolsky; Sarid, 26.4.1950, N. Naftolsky. All, unless stated otherwise, in HUJ.

There can be no doubt that both species are very closely related to each other. As main differential characters we wish to emphasize: the longer calyx teeth of *T. carmeli* with their spreading, strongly tubercled hairs forming an involucre to the heads already in the initial phase of flowering, the denser arrangement of the flowers in the roundish heads which do not become elongate in fruit as in *T. vavi-*

* Erect, spreading-pubescent annual, 10–30 cm high, branching from base. Stipules oblong, with free portion as long as united or longer in the upper leaves. Leaves except the upper pair alternate, lower long-, upper short-petioled, leaflets short-hirsute, obovate, elliptic or rhombic-lanceolate. Heads small, peduncled, loose, in fruit ovate-conical or oblong, echinate by spiny-tipped calyx teeth. Calyx oblong, later on campanulate, with 10 nerves prominent below; tube short (2 mm), hirsute, with lanceolate-linear one-nerved unequal teeth, the lower much broader and — especially in the lowest florets — considerably longer and finally bent outwards; standard oblong, short-stipitate, 2–3 times longer than wings and keel. Fruit obovate. Seeds small, purplish or greenish-yellow.

lovi, and the shape of the standard, which is triangular-caudate instead of oblong-spathulate (Figures 1, 3).

Both species are clearly distinguished from *T. alexandrinum* by their short, strongly ribbed calyces with narrow teeth, and by the spreading, instead of appressed, character of the hairs on their stems and branches. Furthermore, as a rule they are smaller than the Egyptian clover, and are thus hardly so closely related to be considered its nearest wild relatives. However, it must be admitted that *T. vavilovi* resembles *T. alexandrinum* more than *T. carmeli* by its 1) relatively short calyx teeth; 2) a broader standard. It further possesses relatively large seeds covering the same colour range, from reddish-brown to lemon-yellow, as those of the Egyptian clover (Ullmann 1957).

The following Table stresses these facts more clearly.

TABLE I
Main morphological differences between some species of the *alexandrinum*-group

	<i>T. alexandrinum</i>	<i>var. berytheum</i>	<i>T. carmeli</i>	<i>T. vavilovi</i>
Hairiness	Appressed	Appressed	Spreading	Spreading
Calyx shape	Tubular-obconical, widening from base		Oblong, not or little broader at tip	
Calyx nerves	Not prominent at anthesis		Prominent at anthesis	
Calyx size	Large	Small	Small	Small
Calyx teeth:				
(a) breadth	Broad	Medium broad	Narrow	Narrow
(b) length	Short, equal	Short, \pm equal	Long, unequal	Long, unequal
(c) hairiness	Short-hairy	Plumose-hirsute	Long-hispid	Rough to hirsute
Standard	Linear	Linear, finally cuspidate	Long-triangular	Oblong

Ecologically and phytogeographically, both species, which are endemic in Palestine and Syria, differ rather distinctly from each other. *T. carmeli* grows in Mediterranean maquis or garigue, mainly on terra rossa, preferring apparently the conditions of the *Quercus calliprinos*-*Pistacia palaestina* association and eu-Mediterranean climatic conditions. It is thus adapted to more humid and shady conditions than *T. vavilovi*, which seems to avoid the Mediterranean coastal region, occurring mainly in the inner plains, in open localities. It is a semi-segetal species growing under conditions of the eastern border of the Mediterranean area, where stepic influences are felt. The areas of both species seem to overlap at the eastern border of Mt. Carmel and near Mt. Tabor, where *T. vavilovi* is widespread on pastures. While the occurrence of *T. vavilovi* in the Jebel Druze (Mouterde 1953) is not surprising, *T. carmeli*, indicated by Mouterde for the forest of Qanawat and three other localities, is evidently bound there to the Mediterranean *Quercetum calliprini*, and might possibly be regarded as a relic of the Pluvial period (cf. Mouterde 1953, p. 31).

DISCUSSION

Thus, having found little evidence for a derivation of *T. alexandrinum* from the investigated related species of the region of Post's Flora, except *T. berytheum*, it remains to discuss its relationship to Bobrov's *T. apertum*, of which the Herbarium of the Hebrew University possesses co-type specimens from Majkop, province of Krasnodar, No. 3725 of the Herbarium of the USSR. Even a superficial examination shows considerable morphological deviations of this species from *T. alexandrinum* (Figure 8).

- 1) The stipules of *T. apertum* possess long apical "tails", which sometimes are twice as long as their basal portion. In the uppermost pair of leaves, they are narrow, instead of dilated.
- 2) In the early stage of flowering, the calyx teeth are long-lanceolate to linear and narrow, reaching sometimes 5-6 mm in length. That is, they are about $2\frac{1}{2}$ times as long as the tubes. They spread star-like at maturity, while those of *alexandrinum* remain erect, as a rule (later on the teeth-tube proportion diminishes, as a consequence of stronger tube growth). The teeth possess much more pronounced median nerves than those of *T. alexandrinum*.
- 3) The hairs on the outside of the calyx and in its throat are fewer in number and more setose than in *T. alexandrinum*, reaching as much as 1.4 mm in length. The teeth, therefore, look pectinate rather than plumose.
- 4) The corollas are apparently longer, 14-15 mm, according to Bobrov's indications (l. c.).
- 5) The teeth of the apices of the leaflets seem to be more strongly developed, with more of them developing mucros.
- 6) Finally, the inflorescences have longer peduncles from the outset.

While the above differences seem important, we do not wish to deny that both species are indeed quite similar to each other. However, we consider *T. apertum* as belonging to a group of species comprising *T. carmeli* and *T. vavilovi*, from which we wish to separate *T. alexandrinum*, with its numerous strains and varieties. *T. apertum* is indeed very similar to *T. carmeli* in its ecological character, growing on meadows between shrubs, as well as morphologically by the shape and indument of its calyx teeth, which show, however, a tendency towards shortening, except the lower one, which often surpasses by far the others. This tooth is frequently thick and narrow, in contrast to *T. alexandrinum*, where it is often considerably broadened. It should be added that the fruiting inflorescence of *T. apertum* is rather similar in appearance to that of *T. vavilovi*.

The Taxonomic Value and Distribution of T. berytheum Boiss. et Blanche

Thus led back to *T. berytheum* as the wild taxon most nearly related to *T. alexandrinum*, we must at first clearly define what ought to be understood under this name. There are two alternatives: separation of the Palestinian material differing from Boissier's description in his "Diagnoses" (1856, p. 15) by longer peduncles (though not always), and nerveless calyces (when fresh), silky-hirsute from their base, into a separate taxonomic unit; or the uniting of the Lebanese and Palestinian material under the old name of *T. berytheum*, with a slight modification of the original description. We prefer the second solution. Thus we arrive at the following new diagnosis of this microspecies, or rather variety of *T. alexandrinum*, published so far only by Rechinger for Palestine (Israel) in the "Reliquiae Samuelssonianae".

Trifolium alexandrinum L. var. *berytheum* (Boiss. et Bl.) Trab. (1910).

T. berytheum Boiss. et Bl. in Boiss. Diagnoses Ser. 2, 2:15 (1856), emend. Opphr. (Figures 4, 5).

Differs from the Linnaean species by often *small-flowered*, dense, often sessile heads, which are then sheathed by the broadened stipules of the uppermost pair of leaves. After anthesis, they often become elongated, oblong-cylindrical or conical, instead of ovate. Calyx including teeth about 5 mm long, with teeth more thickish and narrow-subulate than in type, densely hirsute by white or (only after drying?) brown hairs in a paint brush-like manner, the hair becoming longer and denser from below; throat of calyx filled with hirsute hairs and teeth plumose with *tuberculate* hairs frequently purplish-violet at limb; standard as a rule narrow, elongated. Seeds small, obovoid, slightly compressed, 1.3 to 1.6×0.8 to 1.3 mm, straw-coloured, Indian yellow or reddish-brown, one end often spread over with green or red.

Remark: If insufficiently ripened, the seeds appear triangular-flattened, the cotyledonary end protruding.

Hab. (in addition to localities mentioned above) AP: Coastal plain, near Acre, 5.5.1927, N. Naftolsky (forma brunneo-hirsuta, with brown calyx hairs, like Blanche's type specimens). Ca: above the Nesher factory, slopes of Mt. Carmel, 5.5.1955, N. Naftolsky. Sh: Hadera, Gazaze swamp, 27.4.1906, A. Aaronsohn (AH 4989; f. brunneo-hirsuta). UG: Kedesh Naftali, fallow field, 27.5.1949, N. Feinbrun. EP: Affule, in irrigated lawn, 11.5.1956, N. Feinbrun; Kefar Yehezkiel, 28.3.1953, M. Zohary.

T. alexandrinum var. *berytheum* prefers moist localities and is apparently unable to grow where rainfall is low, unless local conditions produce high soil moisture.

Remark: While neither Aaronsohn's nor the new Herbarium of the Hebrew University seem to contain true berseem escaped from cultivation, Aaronsohn's No. 5007 is cultivated berseem from the former German Colony Sarona near Tel Aviv, collected on May 22, 1906. It resembles var. *berytheum* by hirsute calyces and preponderantly sessile inflorescences, which are common also in Egypt, to judge from Ibrahim Ramis's key (1929, p. 106), who says of *T. alexandrinum*: "Köpfchen gestielt oder sitzend".

Comparison between alexandrinum and var. berytheum

The main distinguishing characteristics between the Linnaean species and its wild growing variety *berytheum* are the following: the calyx of *T. alexandrinum* is in most cases a little longer, reaching 5 to 7.5 mm in total length, instead of 4-5 in var. *berytheum* (Figure 4). While the calyx tube is whitish below in both, we often find green stripes running down to the base in the berseem. This we did not see in the Beyrouthian clover (Figure 5). The ramifications of the Egyptian clover grown in Israel (mainly the variety Miskawi) grow more upright, its heads reach larger sizes, especially in fruit, and are less compact. In all other respects, and even in those mentioned here, and in one above diagnosis, both merge into one another, so that we must agree with Gibelli and Belli (1888), who, after examining the type specimen of *T. berytheum* at Geneva, wrote on a label seen by Eig (1934) that they could consider this material only as a *T. alexandrinum* with a somewhat more callous throat (a character which we did not find by any means constant!). Other botanists, like Trabut and Thiébaud also considered it as a variety of *T. alexandrinum*. Therefore, though it appears to us not quite satisfactory to consider a wild and probably more ancient race as a variety of a younger, cultivated one, we do not think it justified to follow Eig, retaining both as separate, independent species.

To settle the problem definitely, we needed more information about the variability of the cultivated *T. alexandrinum*, investigated earlier by Mostovoj and Zaitshchek (1937). For first hand information, we collected in May, 1958, flowering specimens at Zarnuqa, a village near Rehovot. Even a superficial look at these plants disclosed the extreme variability of the characters separating the "cultivar" from its wild relative. Thus, not only flowering, but also fruiting heads were quite often sessile and sheathed by the upper pair of leaves as in var. *berytheum* (Figure 10). While we did not observe calyx tubes shorter than 3 mm which were in the flowering stage more tubular than the rather obconical ones of *berytheum* collected in the neighbourhood of Jaffa, pronounced long-hairiness of the calyces reminded one often of the wild variety. There was wide variability in the length of the basal, stamino-vexillar tube of the florets (longer, as a rule in *berytheum*) and the angle of deflection of the standard (more bent backwards, as a rule, in *berytheum*). The standard, instead of being relatively short and broad, was, especially in older florets, often narrow and elongated, as in *berytheum*. In these respects, one could easily find *berytheum* characters in almost every individual. The tip of the standard (eroded or entire) and its colour (pink with red nerves or white) were also variable. Similar variations are found in *berytheum*, and it was interesting to observe in the berseem also the purplish tint of the calyx teeth, so common in *berytheum*.

Figures 4, 5, demonstrating the difference between Alexandrian and Beyrouthian clover in the structure of the flowers (longer calyx tube, shorter and broader

and shorter-stalked standard, shorter stamens in the former) give also an idea of the great variability in length and shape of the calyx teeth. We find parallel variations in both clovers from longer and unequal teeth to short and nearly equal ones, and the comparison of the unanalyzed florets (Figure 5) indicates relatively broader calyx teeth in *berytheum*. This is rather the exception than the rule.

Consultation of foreign and local specimens in herbaria corroborated the conclusion that none of the distinctive characters separating var. *berytheum* from *T. alexandrinum* is of an absolute value. Thus, we found *T. alexandrinum* from Montpellier (France) with short calyx tubes (2 mm), as in *berytheum*, and Swiss *alexandrinum* from the castle Bioley-Manoux (Vaud), leg. P. Villaret, with densely silky-plumose calyces and with paint brush-like tufts of long hairs (1 mm) on their outside. These differed little in this respect from wild material collected by us near Gealyah, Israel, which we propose to designate as forma *sericea* nob. of var. *berytheum* (Diagn. "calyce a basi dense sericeo").

Even in material of *T. alexandrinum* grown in the Variety Collection of the Agricultural Experiment Station of Neve Ya'ar, Israel, in 1955 we found vast differences in the size of the calyces and the breadth of their teeth. The variability of *T. alexandrinum* finds expression also in the number and distinctiveness of the nerves on the lateral teeth, which sometimes have a long median and two distinct lateral nerves running through half of their length or only the median one, which can be rather indistinct. Quite variable also is the breadth of the inferior calyx tooth and the distance between the upper two, which can be united at the base, as stated by Linné in his diagnosis, or separated, leaving a narrow and acute or a broad and obtuse interval between each of them.

The same trends of variability can be observed in var. *berytheum*, and this is true also for a character of great taxonomic importance: the presence or lack of a callosity and of hairs in the throat. Thus, we collected at Rehovot an *alexandrinum* escaped from cultivation without any callous ring and a *glabrous throat*, while apparently wild *alexandrinum*, collected independently by both M. Zohary and N. Feinbrun in the Huleh Plain, was found pronouncedly callous and also completely *glabrous* (Figure 9). While the former character would be more compatible with var. *berytheum*, the latter contradicts decidedly its definition. These specimens look intermediate between *T. alexandrinum* and *berytheum*. If really wild, they certainly deserve special attention as spontaneous *alexandrinum* of a so far apparently unknown character: a two-lipped callosity nearly closing the throat, as in the *Intermedia*-group of *Eu-Lagopus*, in the classification of Gibelli and Belli (1888).

In conclusion, we feel justified in stating that *T. alexandrinum* and its variety *berytheum* present a coherent, uninterrupted complex of morphological characters from which apparently different combinations (unstable types) have been selected

by man and introduced into his fields, where they continue to vary as in their native habitats.

THEORY OF ORIGIN OF THE CULTIVATED EGYPTIAN CLOVER

At the conclusion of the present investigation, we wish to stress that its results corroborate the view of Aaronsohn and Eig that *T. alexandrinum* grows wild in Palestine. They are in close agreement also with the view of Trabut that *T. berytheum* is the wild "form" of *alexandrinum*. On the other hand, we found no evidence of still nearer relatives in Asia Minor or the Black Sea region. The idea that *T. apertum* is the "ancestor" of *T. alexandrinum* cannot be substantiated by our investigation, since present-day types of the Egyptian clover are not essentially different from wild growing ones, and there is no evidence of morphological changes leading from a wild, well-defined plant type, through a series of phylogenetic developments *, to a morphologically different, well-defined cultivated species. This must be understood to be the consequence of the fact that at most a few thousand years have passed since man began to cultivate the "Egyptian" clover in Syria (Damascus?), Palestine and, probably much later, in Egypt. This may have happened in the Bronze or Iron Age or still later. Instead of grazing his animals on the alluvial, swampy meadows of the coastal and inner plains of Syria and Palestine, he selected seeds and grew them in ploughed fields on similar heavy and moist soils, without or (in Damascus and the Nile Valley) with irrigation. For a field crop, he selected and possibly developed types with larger seeds which germinate easily, in contrast to the wild growing varieties which evince a very low germination capacity, at least when sown in the season following their maturation.

The process which we visualize here is completely analogous to the situation with other clovers, like Red and White Clover. The latter, *T. repens* L., also a very polymorphous species, has developed in culture slightly aberrant types, like the Dutch and the Ladino clovers. The species grows in the neighbourhood of Jaffa, as well as in the Huleh Plain, where we encounter a gigas-type with very large leaves, resembling Lodi (Ladino) clover and possibly identical with var. *giganteum* Lagr.-Fosset. This local type has been successfully tried out in Israel as a field crop, during the last few years. Quite an analogous process probably took place, with *T. alexandrinum* starting from the same localities a few thousand years earlier and, in this or other countries, with other clovers which differ little in culture from their wild-growing types, like Red and Persian clover, *T. fragiferum* and *T. subterraneum*.

Zhukovsky (1957), in his recent survey of the origin of cultivated plants, distinguished between two main groups: one developed directly from a wild species,

* Certainly there is no justification to suggest a wild *extinct* prototype, an idea advanced by Kennedy and Mackie (1925).

and another one of hybrid origin. In the first one, the cultivated species developed from the wild one by domestication and selection of mutants. Evidently the case of *T. alexandrinum*, like that of *T. pratense* cited by Zhukovsky, is typical of the first group.

The intercourse of populations between Egypt, Palestine and Syria has always been considerable enough that a plant grown in one country could easily be introduced into one of the others. It seems only natural to assume that from habitats around Jaffa, the Phoenician coast, the Huleh Plain, or possibly Lake Phiala, the cultivation of the Alexandrian clover spread northeastward to Damascus (according to Zemach, l.c.), a centre of its cultivation. On the other hand, it might have reached the Nile Valley through the oases of the Isthmus Desert, like El-Arish. There it attained remarkable proportions in agriculture, as the main soiling and forage crop of the Egyptian peasant, covering in that country nearly one million hectares in the yearly rotation.

INTERBREEDING PROBLEMS

If the wild *T. alexandrinum* is essentially identical with cultivated berseem, it could be expected to interbreed freely with it under field conditions. The striking frequency of involucrate heads in the irrigated fields of the Philistaeon Plain between Rehovot and Yavneh (Yibna), in our time as well as early in this century in the fields of the German colonists seems to underline such a possibility, which would probably lead also to great fluctuations in seed size, actually known to occur in Egyptian clover (Ullmann 1957). However, we doubt if, in fact, such interbreeding is a widespread phenomenon, even in localities where berseem fields are surrounded by uncultivated strips or tracts harbouring *berthoum*. Since the cultivated berseem is periodically cut and, at least in Israel, irrigated, ripe seed is produced only late in the season (about June). Thus, when it is allowed to flower, the wild plant is no longer in bloom, but dries up and bees or butterflies (*Lycaenidae*) visiting the berseem, no longer can effect hybridization. As stated before, we have further observed that the wild *T. alexandrinum* soon disappears under conditions of drainage and cultivation. It is choked out by strong growing summer and winter weeds, which produce much more seeds of much higher germination capacity.

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POST SCRIPTUM

Ullmann (1957-58) suggests Mesopotamia as the country of origin of the berseem and opposes the view of a Syrian-Palestinian origin, without any cogent evidence. We are unable to discuss this contribution at present.

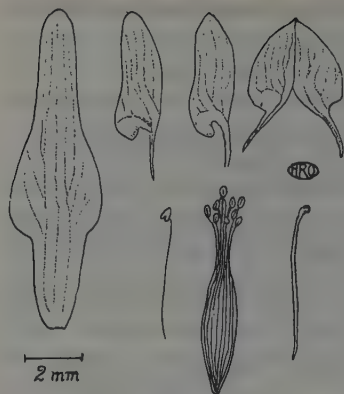


Figure 1
Trifolium carmeli Boiss.; analysis
of the flower.



Figure 2
T. carmeli Boiss.; calyx opened,
inside view.

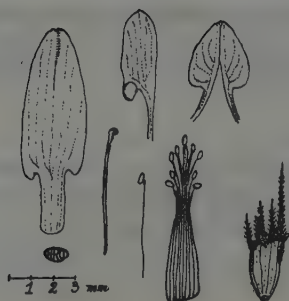


Figure 3
T. vavilovi Eig; component parts
of the flower.

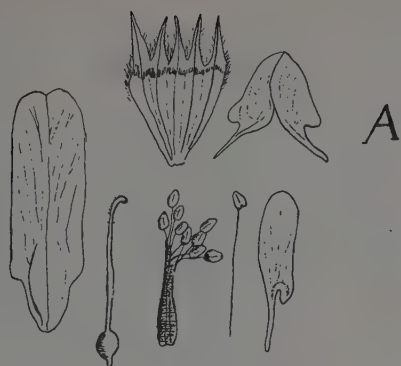


Figure 4

T. alexandrinum L.; type cultivated (A) and var. *berytbeum* (B); analysis of flowers, both with abbreviate calyces.

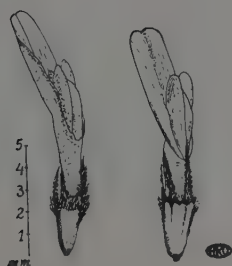
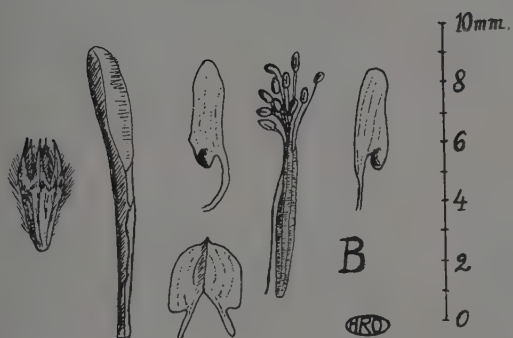
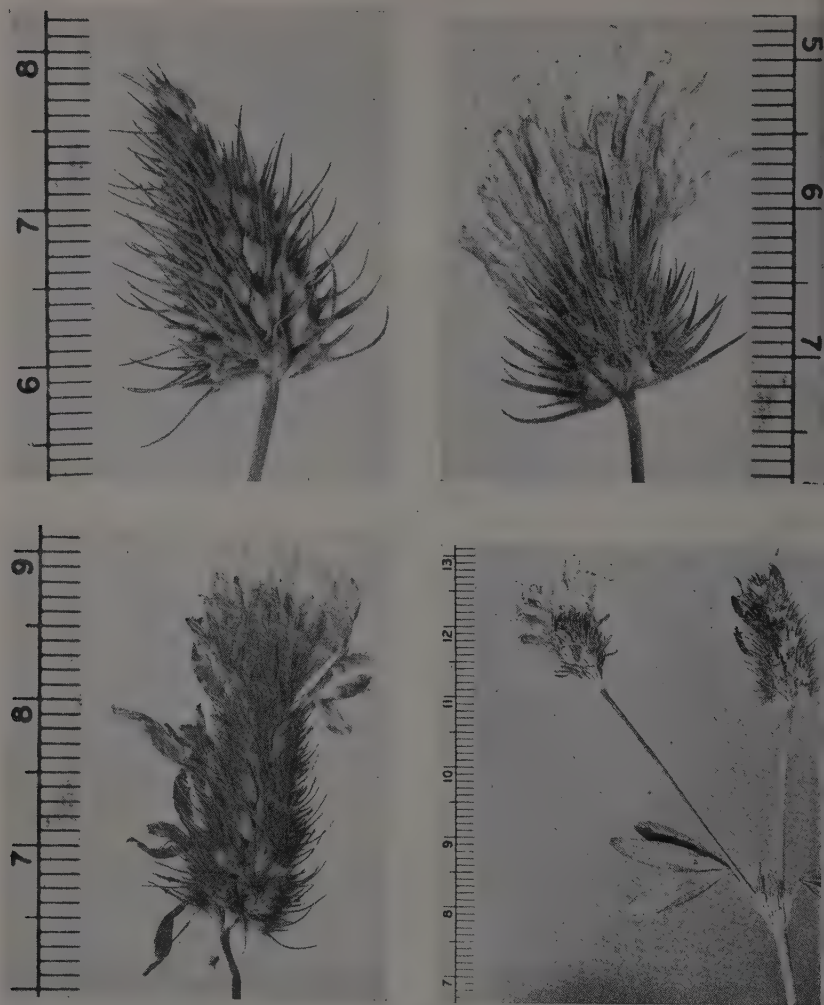


Figure 5

Florets of *T. alexandrinum* L. *typicum* (right) and var. *berytbeum* (Boiss. et Bl.) Dinsm. (left).



Figures 6-9. Inflorescences of clovers of the *alexandrinum* group.

Figure 6. *Trifolium vavilovi* Eig. Figure 7. *T. carmeli* Boiss. Figure 8. *T. apertum* Bobr.
 Figure 9. *T. alexandrinum* L. with glabrous, callous throat collected by M. Zohary in the
 Upper Jordan Valley (Huleh).

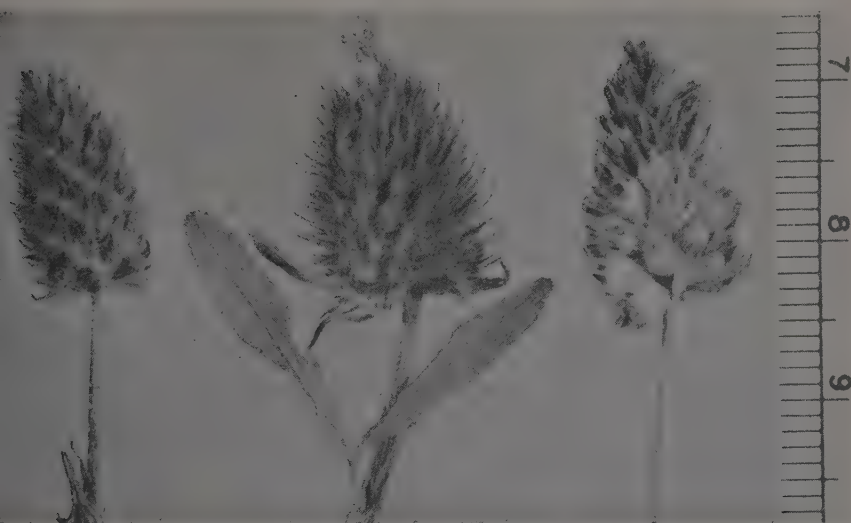


Figure 10. Fruiting heads of *Trifolium alexandrinum*.

Right to left: Fully mature, large seeded cultivated variety; half-mature cultivated variety with 2 supporting opposite leaves; fully mature wild variety *berytbenm* without pair of sheathing leaves.

A CONTRIBUTION TO THE KNOWLEDGE OF HIGHER FUNGI OF ISRAEL*

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ABSTRACT

32 higher fungi were determined of which 3 belong to the Aphyllophorales, 4 to Boletales, 2 to Asterosporales, 17 to Agaricales and 7 to Gasteromycetes. The paper includes a new species, *Tricholoma weizianum* and 2 new varieties, *Crepidotus variabilis* (Pers. ex Fr.) Quel. var. *stercorarius* and *Lepista sordida* (Fr.) Sing. var. *gracilis*.

Mention has been made of the different ecological conditions prevailing in Israel bringing about seasonal changes in the appearance of the various fungi.

INTRODUCTION

The climate of Israel may be described as being Mediterranean in the northern and central area, particularly along the coastal plain and in the mountains, becoming increasingly more arid towards the east and in particular towards the south. The larger part of the Negev expanses is truly desert in character. The most noticeable feature of Israel climate is the almost complete lack of rain from April to November, leaving the winter months as the rainy season. The transitional seasons, spring and autumn, between the dry and the wet, are very brief, unlike those of central and northern Europe.

Observations made in Israel show that the time in which the sporophores of higher fungi make their appearance corresponds very closely with the rainy season. Generally, mushrooms begin to appear by the middle of November or at the end of this month after rain has fallen a number of times and in sufficient quantities to saturate the dried-out soil. There are a few notable exceptions, e.g. *Xerocomus silveriana* Reichert (unpublished), a mushroom growing in soils with high water-table, which appears soon after the first rain.

The season of the abundance of higher fungi terminates in March after the appearance of hot dry spell called "Khamseen". During the rainy season, there may be periods in January and February when sporophores do not appear because of freezing temperatures. In summer, as mentioned, agarics do not generally appear, with few exceptions, e.g. *Chlorophyllum molybdites* (Meyer ex Fr.) Mass. (*Lepiota morgani*) (Reichert and Avizohar-Hershenzon 1953), which seems to be of tropical origin.

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This paper is a new contribution to the knowledge of higher fungi on which several papers have already been published (Avizohar-Hershenzon 1953; Reichert 1940a, 1940b, 1944; Reichert and Avizohar-Hershenzon 1939, 1955; Rayss and Reichert 1952). It comprises 32 fungi belonging to Hymenomycetes and Gasteromycetes. Three of them are newly described: A new species, *Tricholoma weizianum*, and two new varieties, *Crepidotus variabilis* (Pers. ex Fr.) Quel. var. *stercovarius* and *Lepista* (*Rhodopaxillus*) *sordida* (Fr.) Sing. var. *gracilis*. Our list contains one poisonous mushroom, *Omphalotus* (*Pleurotus*) *olearius* (DC. ex Fr.) Sing. Other poisonous mushrooms, like *Amanita verna* (Lam. ex Fr.) Pers. and *Chlorophyllum molybdites* (Meyer ex Fr.) Mass. (*Lepiota morgani*) have been described elsewhere (Avizohar-Hershenzon 1953).

Most of the fungi described in this treatise, as well as others listed in other publications are not found in Europe. Among these are some which are indigenous to the Mediterranean area, e.g. *Amanita boudieri* Barla and *Amanita ovoidea* (Bull. ex Fr.) Quél. A fair number of species appears here which are found in northern Europe, but which fruit here during a different season of the year; these mushrooms apparently find conditions which do not differ greatly from those found there at the time of their fruiting. Mention may be made of *Amanita vaginata* (Bull. ex Fr.) Quél. which appears in Europe in June–November and here in March–April, *Tricholoma albobrunneum* (Pers. ex Fr.) Quél. in September–November in Europe and here in January–February, *Stropharia coronilla* (Bull. ex Fr.) Quél. in May–October in Europe (Rea 1922) and in December–January here. Slight differences in habitus often exist between the same species here and in Europe. These differences are, so it seems, the result of slightly different ecological conditions and/or of a geographical isolation as has already been pointed out by Malençon (1951), who found slight differences between species of the Middle Atlas of Morocco and the same species in Europe. Present here are *xerophytes*, which are found in Europe (Alexandri 1934, Hollos 1903, Petri 1909) also under arid conditions. Among these are *Battarea guicciardiniana* Ces., *Montagnites candollei* Fr. growing on sand dunes or in the vicinity of the southern desert.

Some of the fungi are associated with some higher plants here. They fall into two categories: Fungi which are associated with indigenous plants, and those which are found together with introduced ones. To the first category belongs *Tricholoma albobrunneum* (Pers. ex Fr.) Quél., *Ixocomus* (*Boletus*) *granulatus* (Fr. ex L.) Quél. which are always found together with *Pinus halepensis* and *Pleurotus eryngii* Quél. var. *ferulae* (Lanzi) Sacc. which grows in close connection with *Ferula communis*. In the second category, mention may be made of *Pisolithus tinctorius* (Mich. ex Pers.) Coker et Couch, which is connected with *Eucalyptus* as it is also in South Africa (Bottomley 1948).

The systematic arrangement of the groups and families in this treatise follows that used by Heim (1957). The nomenclature of the genera and species of Agari-

cales is used according to Singer (1949). The Gasteromycetes are named according to Bottomley (1948).

The colours in quotation marks were taken from Ridgway (1912).

APHYLLOPHORALES

Fam. POLYPORACEAE

Caloporus leucomelas (Fr. ex Pers.) Quél. (Plate I figure A)

Fl. Myc. Fr.: 405. 1888.—*Polyporus leucomelas* (Pers.) Fr. Syst. Myc. 1:346. 1821.—*Boletus leucomelas* Pers. Syn. Meth. Fung.: 515. 1801.

Under *Pinus halepensis*. Ca*: Beth Oren, 350 m, 31.12.1941 W, 5.1.1954 A. Yolles.

Spore sizes in our specimens (3.75) 4.5–5.25 (6) $\mu \times$ (3) 3.75–4.5 (5.25) μ .

Fam. CLAVARIACEAE

Clavulina cinerea (Fr.) Schroet. (Plate I figure B)

Krypt. Fl. Schles. Pilze: 449. 1888.—*Clavaria cinerea* Fr. Syst. Myc. 1:468. 1821.

Plants growing solitarily in a *Quercus calliprinos* wood. Ca: Wadi Shumriye, 75 m, 12.2.1956 W.

The colour of our specimens was brownish-gray with a tinge of violet ("Light Brownish Drab" and "Wood Brown") or "Benzo Brown". Spore sizes $6.75\text{--}9\mu \times 6\text{--}7.5\mu$. Basidia mostly two-spored and $5.25\text{--}7.5\mu$ thick; sterigmata $5.25\text{--}6\mu$ long.

Corner, in his monograph *Clavaria and Allied Genera* (1950), enumerates various forms and varieties of *Clavulina cinerea*; it seems that our specimens resemble the type of the species.

Fam. CANTHARELLACEAE

Cantharellus cibarius Fr. (Plate I figure C)

Syst. Myc. 1:318. 1821.

In mixed forest of *Pinus halepensis* and *Quercus calliprinos* (but found under *Q. calliprinos*) in terra rossa soil, Ca: Mt. Carmel, 500 m, 8.12.1951 W.

BOLETALES

Fam. BOLETACEAE

Xerocomus chrysenteron (Bull. ex Fr.) Quél. (Plate I figure D)

Boletus chrysenteron Bull. Cham. Fr.: t.490 f.3. 1790.

*ABBREVIATIONS—*Districts*: Ca=Mt. Carmel; CN=Central Negev; EV: Esdraelon Valley; J: Judean Mountains; LG: Lower Galilee; P: Philistaeen Plain; Sh: Sharon; She: Shefela; UG: Upper Galilee; UJ: Upper Jordan Valley.

Collectors: H=Zehara Avizohar-Hershenzon; CI=Tamar Itinzon; Rs=Tscharna Rayss; Rt=I. Reichert; W=H. Weiss; Z=M. Zaharoni.

In *Quercus calliprinos* woods. In terra rossa soil, Ca: Beth Oren, 350 m, 22.12.1951 W, 11.12.1953 W, H; EV: Kiryat-Amal, 125 m, 8.12.1951 Z; Alonim 120 m, 14.12.1951 Z.

Because of the unclear distinction between *X. chrysenteron* and *X. versicolor* and the great variability of both species, we are giving a full description of our specimens.

Pileus 3–9 cm broad, convex then convexo-plane, irregular in shape, dry, subtomentose, chocolate brown ("Cameo Brown") or copper reddish-brown ("Vandyke Red"), surface often irregularly cracking showing beneath the reddish flesh, if deeper cracked the yellow flesh appears. Tubes 4–6 mm long "Aniline Yellow", when rubbed or cut turning dirty yellowish-green, irregularly sinuate; when approaching the stipe lamella-like, these lamelloid tubes are shortly decurrent on the stipe. Orifice of pores "Aniline Yellow", when rubbed turning yellowish green ("Citrine"), angular, elongated. Stipe solid, thin, curved 4–8.5 cm × 8–15 mm, narrower near the apex, tapering from the middle part downwards to a very narrow base; yellow and slightly pruinose above, fibrous with a vinaceous-reddish colour below, this reddish colour tending to spread with age towards the apex; yellow fresh parts of the stipe turning greenish when rubbed, while the vinaceous-reddish parts remaining unchanged or darkening slightly. Flesh in the pileus "Baryta Yellow", "Amber Yellow" or "Empire Yellow", but just below the cuticle vinaceous-reddish; between the reddish stratum and the cuticle a very thin yellow strip may sometimes be seen; flesh in the upper part of the stipe is yellow, concolorous with that of the pileus, the lower part, especially the base, shows a reddish-vinaceous colour which with age becomes dominant in all the stipe; the yellow part in the pileus and the stipe turns blue when cut. Spores 11.25–13.25 (15) μ × 5.25–6 (7.25) μ , subfusiform. Tastes very good.

According to Gilbert (1931), Maublanc (1946), Rea (1922), Wakefield and Dennis (1950), the following features seem to be more or less distinctive between these two species and they are compared in Table I with our specimens:

All the above-mentioned features (Table I) seem to point out that our specimens belong to *X. chrysenteron*.

***Boletus queleti* Schulz var. *lateritus* Bres. et Schulz** (Plate I figure E)

Myc. Beit: 1885.

In calcareous soils under *Quercus calliprinos* trees. UG: Wadi Taibe, 22.12.1951 W.

The colour of the pilei of our specimens "Jasper Pink" or "Light Corinthian Red", mingled in some places with "Chamois" patches; the rubbed places becoming darker due to the blackening of the fibrils. The orifice of the spores which were of "Dragon's-blood Red" or "Hay's Russet" colour became with age "Vinaceous-Rufous"; this red colour was not uniform but mingled with yellow patches. The "Mustard Yellow" or the "Naples Yellow" or the upper part of the stipe passed gradually to reddish ("Ochraceous Salmon") in the lower part; with age

TABLE I

Morphological differentiation between X. chrysenteron, X. versicolor and our specimens

Fungus	Pileus	Stipe	Flesh under the cuticle
<i>X. chrysenteron</i>	Tendency to crack. Colour brownish, copper-red or brownish-red	Fibrous and striate	Reddish
<i>X. versicolor</i>	Without tendency to crack (?). Colour rose red	Pruinose and minutely granular	Not reddish
Our specimens	Tendency to crack. Colour chocolate-brown ("Cameo Brown") or copper-reddish-brown ("Vandyke Red")	Fibrous	Narrow stripe under the cuticle reddish

there was a tendency of the flesh to redden ("Jasper Pink", "Pompeian Red"). In this stage the fungus did not change to blue upon cutting, a character which was observed in the young and fresh parts. The spore sizes $9-10.5 \mu \times 4.5-5.25 (6) \mu$.

Fam. PAXILLACEAE

Paxillus panuoides Fr.

(Plate I figure F)

Epicr.: 318. 1836-1838.

Very common on dry branches or stumps of cut down *Pinus halepensis* trees. Ca: Beth Oren, 350 m, 24.1.1952 W; P: Ramat-Gan near Tel Aviv, 50 m, 2.2.1952 G. Kowatch; Rehovot, 50 m, 17.1.1952 S. Gazith; EV: Kiryat Amal, 125 m, 1.3.1952 Z. Frank; She: Hulda (Coastal Plain close to the Judaeen Mountains), 125 m, 23.2.1952 H; J: Sha'ar-Hagai, 300 m, 4.2.1952 H. Once found on sawdust of imported *Pinus silvestris* wood, Rehovot, 1.1.1956 H.

The colour of the pilei of our specimens was "Chamois" or "Honey Yellow" with darker patches of "Isabella Color" or blackish patches. The colour of the lamellae "Light Ochraceous-Buff" then "Ochraceous Orange." The flesh dirty cream when fresh, turned whitish upon drying, 4-5 mm thick, swelling up to three times its size when soaked in water; under ammonia vapour became yellow-ochre with a narrow, 1 mm, violet stripe of "Slate-Violet" beneath the cuticle. Spores $4.5-6(7.5) \mu \times 3.75-4.5 \mu$, "Clay Color" in mass.

Fam. GOMPHIDIACEAE

Gomphidius viscidus (Linn.) Fr.

(Plate II figure A)

Monogr. Hym. 2: 150. 1857-1863. — *Agaricus viscidus* L. Sp. Pl.: 1173. 1753.

In *Pinus halepensis* forest, Ca: 650 m, terra rossa soil, 22.12.1951 W; J: Kiryat Anavim, 700 m, 13.12.1950 Rt.

The pilei of our specimens are smaller, 2–5 cm in diameter, than those described for *Gomphidius viscidus* by Saccardo (1916), Maublanc (1946), Rea (1922) and Ricken (1915), 5–8 cm, 5–10 cm, 5–15 cm and 5–10 cm, respectively; but they approach the size given by Lange (1935–40) for his "typical" form, 4–7 cm or more. According to Lange the larger specimens belong to the form "giganteus". The spores of our specimens which measure $15\text{--}18\ \mu \times 6.5\text{--}7.5\ \mu$ seem to be a little shorter than the length given by the above authors as $16\text{--}42\ \mu$.

ASTEROSPORALES

Fam. RUSSULACEAE

Lactarius deliciosus L. ex Fr. (Plate II figure B)

Epicr.: 341. 1836–1838. — *Agaricus deliciosus* L. Sp. Pl.: 1772. 1753.

In *Pinus halepensis* forest mixed with *Quercus calliprinos* and *Pistacia* spp. bushes. Ca: 400 m, 6.1.1950 W, 18.10.1951 W; J: Kiryat Anavim, terra rossa soil, 700 m, 16.1.1941 H & H. Habelska, 10.12.1951 Rt; Rusheni near Hebron, 4.1.1941 Rt, H.

Spores of our specimens were $7.5\text{--}9\ \mu \times 6.75\text{--}7.5\ \mu$, white in mass. Cheilostidia $25\text{--}30\ \mu \times 4.5\ \mu$, fusiform-subulate.

Russula alutaceae (Pers.) Fr. sensu Schaeffer (Plate II figure C)

Epicr.: 362. 1836–1838.—Schaeff. Monog. Ann. Myc.: 399. 1933.—*Agaricus alutaceus* Pers. Syn. Meth. Fung. 441. 1801.

In a wood of *Pinus halepensis* and *Quercus calliprinos* trees, in terra rossa soil. Ca: Beth-Oren, 350 m, 10.1.1953 W.

The spore sizes of our specimens were $7.5\text{--}11.25\ \mu \times 6\text{--}8.25\ \mu$.

AGARICALES

Fam. TRICHOLOMACEAE

Pleurotus eryngii (DC.) Qué. var. *ferulae* (Lanzi) Sacc. (Plate II figure D)

Syll. 5: 347. 1873.

In brown rendzina soil. She: Hulda, 125 m, first collected on 15.12.1951 H; in mixed wood of *Pinus halepensis* and *Schinus molle* trees, in which *Ferula communis* is very common; it was never found in connection with *Ferula communis* outside the woods. Since the above-mentioned date we found it every year from December to February.

Caespitose in groups of 2–3 (7). Diameter of the pileus (3–15 cm) was always longer than the length of the stipe (2–6 cm) and its shape irregular, mostly oval or oblong, sometimes dimidiate. Shade of colour varying from pale brown to dark brown in young specimens ("Cinnamon-Brown", "Natal Brown", "Verona Brown" or "Mummy Brown"), then paler "Buckthorn Brown", or "Ochraceous-Tawny" and finally in grown up specimens "Light-Buff". Spores $9\text{--}15.5\ (16)\ \mu \times 4.5\text{--}6\ \mu$, white in mass. Basidia $45\text{--}50\ \mu \times 8.25\text{--}9\ \mu$ with long sterigmata

up to 7 μ . Generally odourless, occasionally with a slight pineapple smell. Eaten and very much appreciated in the region.

Pleurotus salignus (Pers.) Quél.

(Plate II figure E)

Champ. Vosg. 2 : 843. 1873.—*Agaricus salignus* Pers, in Hoffm. Abb. d. Schw. 3 : t. 29. 1790.

On a trunk of a dead *Parkinsonia* tree. EV : Kfar Tabor, 23.12.1954 S. Gazith.

According to Rea (1922) and Ricken (1915), *Pleurotus salignus* differs distinctly from *P. ostreatus* and is a good species because of (1) the lack of anastomosis of the lamellae; (2) the villosity of the whole stipe; (3) the width of the spore which is narrower 3–4 μ in *P. salignus*, while it is 4.5–6 μ in *P. ostreatus*; but Konrad and Maublanc (1948), Lange (1914–1938, 1935–1940), Kuehner and Romagnesi (1953), and apparently also Singer (1949), consider it only as a form or a variety. Because of these different opinions, we are giving here a full description of our specimens.

Pileus 12–22 cm broad, colour gray-brown or ochraceous-gray; conchate dimidiate with a lobed margin, hygrophanous, glabrose, villose near the very short stipe. Caespitose and partly covering one another. Lamellae up to 15 mm broad, straw coloured, decurrent down to the base of stipe. Stipe lateral, very short, 3–6 \times 3–4 cm, solid, cream coloured, tomentose-strigose. Flesh white. Spores 9.75–11.25 $\mu \times$ 3–3.75 μ cylindrical; colour in mass pale lilac ("Pallid Purple-Drab").

From our description it can be seen that our specimens show the three features which make them distinct from *P. ostreatus*. We, therefore, think that *P. salignus* can be considered a good species.

Crepidotus variabilis (Pers. ex Fr.) Quél. var. **stercorarius** var. nov.

(Plate III figure A)

Ab specie differt cheilocystidiis angustioribus, 4–4.5 μ , nec ut in typo 6–12 μ latis. Hab. ad stercora nec ut in typo ad plantas putridas.

On dry horse manure, 1–5 specimens on each clod in a wood. She : Hulda, 14.1.1953 H.

Pileus 0.5–3 cm broad, sessile, conchoid, reniform, convex, depressed near the attachment to the substrate, slightly undulate, white, tomentose, near the base villose-strigose; margin lobed, slightly inrolled, becoming slightly striate when old. Lamellae whitish, ("Cinnamon Buff") gradually changing to "Clay colour", 1–3 mm broad, subdistant, edge entire; lamellulae in great number. Flesh white, 1–1.5 mm thick. Spores 5.25–6.75 $\mu \times$ 3.37 μ , ellipsoid, minutely punctate; cheilocystidia claviform and subfusiform, 30–39 $\mu \times$ 3–4 μ , thin-walled (Figure 1). Mycelia with clamp connections. Basidia 15–20 $\mu \times$ 4.75–5.25 μ .

Differs from the type species as described by Ricken (1922) and by Pilat in

his monograph (1948) by: (1) Cheilocystidia which are narrower $3-4.5\ \mu$, while they are $6-12$, in the type; (2) the habitat which is clod manure while the type's habitat is decayed plants.



Figure 1

***Mycena pura* (Fr. ex Pers.) Quél.**

(Plate III figure B)

Champ. Vosg. 1:103. 1872. — *Agaricus purus* Pers. Syn. Meth. Fung.: 339. 1801.

Under *Pinus* sp. trees, Mt. Carmel, 20.3.1953 W; under *Pistacia* sp. bushes in a *Quercus calliprinos* wood in a wadi (about 159 m) on the slopes of Mt. Carmel, 14.1.1954 W.

It seems that the spores of our specimens were a little shorter, $4.5-6\ \mu$, than those of Saccardo (1915) which measured $6-8\ \mu$.

***Omphalotus olearius* (DC. ex Fr.) Sing.**

(Plate III figure C)

Agaricales: 181. 1949. — *Pleurotus olearius* (DC.) Gill. Champ. Fr.: 344. 1874. — *Agaricus olearius* DC. Fl. Fr. 6:44. 1815.

Caespitose, attached to the base of olive trees. Ca: vicinity of Haifa, November 1955 sent by Health Office; P: Rehovot, 50 m, 18.12.1955 H; She: Hulda, 125 m, 10.12.1954 R. Kenneth; J: unknown substrate, Jerusalem, December 1950 sent by Health Office.

The specimens which we collected in Rehovot were caespitose in great groups of 7-8 specimens or more the beautiful "Xanthine Orange" colour in the centre of the pileus passed gradually towards the margin into a "Chestnut" brown colour. The "Orange Buff" stipe became darker, "Burnt-Siena", when old or rubbed. Phosphorescence of the lamellae was distinctly observed on fresh specimens. Flesh "Pale Orange Yellow" colour unchanged when cut but turned orange-ochre ("Mars Yellow") when scratched by a nail. With a special sweet smell. This fungus collected in Jerusalem and Haifa caused a number of gastrointestinal poisoning.

***Lepista nuda* (Bull. ex Fr.) W. G. Smith**

(Plate III figure D)

Ex Sing. Agaricales: 193. 1949. — *Rhodopaxillus nudus* R. Maire, Ann. Myc. 11:338. 1913. — *Tricholoma nudum* (Bull.) Quél. Champ. Vosg.: 82. 1872. — *Agaricus nudus* Bull. Champ. Fr.: t. 439. 1789.

Single or gregarious, common in different parts of the country; in various soils (calcareous soils, loams, light sandy soils, etc.) at different altitudes (Kiryat Anavim, 700 m; Rehovot in the Coastal Plain, 50 m, etc.) under different conifers and frondose trees, in woods and under hedges; December-February.

Flesh in the pileus spongy, 10–15 (25) mm thick, lilac, near the cuticle slightly darker, becoming paler upon drying. Inner part of the stipe spongy and lilac while the outer part is fibrous and its colour darker ("Vinaceous Gray"). Spores $5.25\text{--}7.5\ \mu \times 3.75\text{--}5.25\ \mu$, "Pale Cinnamon-Pink", "Pale Pinkish Cinnamon", and "Pale Pinkish Buff" in mass, finely verrucose, non-amyloid.

Lepista sordida (Fr.) Sing.

(Plate IV figure A)

Agaricales: 193. 1949. — *Rhodopaxillus sordidus* R. Maire, Ann. Myc. 11: 338. 1913. — *Tricholoma sordidum* (Fr.) Quél. Champ. Vosg. 1: 84. 1872. — *Agaricus sordidus* Fr. Syst. Myc. 1: 51. 1821.

Densely gregarious and caespitose with many deformed individuals. In brown-red sandy soil under *Thuja* bushes, P: Rehovot, 50 m, 23.1.1945 H.

Flesh 4–12 mm thick (near the stipe), whitish. Spores $5.25\text{--}6.75\ \mu$, pale pink in mass, echinulate, not amyloid. Basidia $22\text{--}27\ \mu \times 5.25\text{--}7.5\ \mu$; sterigmata $2.5\text{--}3.75\ \mu$ long.

Ricken (1915) and Lange (1935–1940) described *L. nuda* as not hygrophanous and *L. sordida* as hygrophanous, but this feature is misleading because *L. nuda* is very often moist, bordering on hygrophanity. More distinct differentiate features, according to our observations which are also mentioned by Lange (1935–1940), Rea (1922), Ricken (1915), Singer (1949), Smith (1949), etc., are: (1) The slenderness of the stipe of *L. sordida*; (2) The colour of *L. sordida* is duller than that of *L. nuda* which is more violet; (3) The disc of the pileus in *L. nuda* is not umbonate; (4) The margin of the pileus of *L. nuda* is mostly inrolled while in *L. sordida* only incurved; (5) The margin of *L. nuda*, even when moist, does not show a striate structure, while in *L. sordida*, which is distinctly hygrophanous, the margin is mostly striate; (6) Flesh of *L. sordida* is thinner; (7) *L. sordida* is caespitose, while *L. nuda* grows solitarily.

Lepista sordida (Fr.) var. *gracilis* var. nov.

(Plate IV figure B)

Ab specie differt statura minore et delicatiore, carne delicatiore, sterigmatibus brevioribus, $1.5\ \mu$, nec ut in typo $2.5\text{--}3.7\ \mu$ longis.

Caespitose, in groups of two or three specimens. Under *Acacia* sp. trees. In sandy soil. P: Rehovot, 50 m, 13.1.1956 F. Littauer; 22.1.1956, 6.2.1956 H.

Pileus 1.5–3 (5) cm broad, convex, then plane, slightly umbonate, margin slightly inrolled when young, with age sometimes wavy and elevated, glabrous, hygrophanous; when young striate and lamellae showing through; grayish lilac ("Pallid Purple-Drab") or lilac ("Grayish Lavender"), umbo brownish ("Avellaneous"), with age the whole pileus becomes entirely "Avellaneous"; upon drying becoming paler, "Pale Pinkish Buff" or "Tilleul Buff". Lamellae adnate, sometimes emarginate or decurrent, slightly arcuate, 2–4 (5) mm wide; edge entire; colour lilac ("Grayish Lavender") then lilac gray ("Pallid Vinaceous-Drab"). Stipe

1.5–3 cm long, 3–6 mm thick, curved near the base, subequal, cylindrical, fibrous, pale lilac ("Lavender" or "Grayish Lavender") becoming brownish ("Avel-laneous"), upon drying becoming pale; solid. Flesh whitish with a lilac tinge, 2–3 mm, thick near the stipe. Spores (4.5) 5.25–6 (7.5) $\mu \times 4.5$ –6 μ broad, oval, very finely verruculose, not amyloid, pink-cream in mass. Basidia 22–25 μ long, (3.75) 4.5–6 μ thick, tetra-spored; sterigmata short (up to 1.5 μ).

Our fungus differs from *L. sordida* by: (1) being smaller and more delicate; (2) the stipe and the flesh of the pileus which are much thinner; and (3) the sterigmata which are shorter, up to 1.5 μ , whereas they are 2.5–3.75 μ in our specimens of *L. sordida*.

Tricholoma weizianum sp. nov.

(Plate IV figure C)

Pileo 2.7–7 (9) cm longo, convexo-gibboso dein de subplano-undulato, fragili, saepius radialiter fisso, fusco, fibrilloso-villoso, in juventute cortina distincta praedito; margine inflexo. Lamellis emarginatis, stipito 5–7 cm \times 8–15 mm, apice pruinoso ad basim villosa. Basidiis sterigmatibus binis usque ad 7.5 μ longis praeditis. Sporis 6.75–9 $\mu \times 4.5$ –6 μ in massa albis.

Caespitose, common in *Pinus halepensis* forest. In brown rendzina soil, P: Ben Shemen 150 m, 14.2.1947 I. Wahl, 14.2.1957 Z. Frank; J: In terra rossa soil, Jerusalem, 700 m, 15.1.1941 H. 12.2.1944 H.

Pileus 2.5–7 (9) cm broad, convex-gibbose, finally subplane and wavy; with or without a small irregular umbo; brittle, often splitting radially; with an inrolled margin and a distinct cortina when young; brownish-gray ("Fuscous"); densely fibrillose-villose. Lamellae gray or whitish, sometimes with white veins; emarginate, with a short decurrent tooth; up to 14 mm wide; subdistant (55–70 lamellae reach the stipe). Stipe 2.5–7 cm long, 8–15 mm thick, white subcylindrical, sometimes flattened, often bent, sometimes twisted, silky fibrous, slightly villose near the base, somewhat pruinose at the apex, solid, with age occasionally slightly hollow; rooting in a rich white thick mycelium. Flesh white, in the pileus very thin — up to 4 mm; in the stipe silky fibrous; without any special taste or smell; edible. Spores (6) 6.75–8.25 (9) $\mu \times 4.5$ –6 μ , white in mass. Basidia (4.5) 6–7.5 μ thick, mostly two-spored or one-spored, with long sterigmata up to 7.5 μ (Figure 2). Cheilocystidia basidiiform, pale brown, 28–30 $\mu \times 4.5$ –6 μ in large groups (see Figure 3). Epicutis pilose, in young specimens 50–150 μ thick, in older ones thinner and discontinuous; it consists of pale grayish-brown, septate, loosely interwoven hyphae, 4.5–7.5 μ thick, which rise towards the surface of the pileus. Subcutis of "cutis-like structure" (Singer 1949), 50–100 μ thick, consists of hyphae; arranged approximately parallel to the surface; in its upper part the hyphae are 6–9 (13.5) μ broad, paler and somewhat more loosely interwoven than those below, which are deep brown and thinner, 4.5–7.5 μ . Hypodermium 35–70 μ thick, consists of pale hyphae, arranged approximately parallel to the surface, looser than

in the subcutis; below, the hyphae become irregular and loose as they pass gradually into the context.



Figure 2



Figure 3

Our species resembles *T. bisporigerum* described by Lange (1914-1938). Both species possess two-spored basidia and very long sterigmata. It differs from *T. bisporigerum* by: (1) the villosity of the pileus, the pileus of *T. bisporigerum* being according to Lange only "minutely felty and slightly squamulose"; (2) the villosity at the basic part of the stipe, a feature not mentioned by Lange; (3) the occurrence of a distinct cortina at younger stage; Lange relates that *T. bisporigerum* "Seems to be without a cortina, but I have not seen quite young specimens"; (4) by the pronounced distinction of ecological habitats, *T. bisporigerum* had been found by Lange in a mossy ground of *Fagus* woods, whereas our specimens are always connected with the Mediterranean xerophilous Aleppo pine forests.

In its macroscopic features our fungus resembles *T. terreum* (Schaeff.) Bres. and *T. myomyces* (Pers.) Lange, particularly the latter because of its cortina which is mentioned by Lange (1935-40); from both it differs by the presence of two-spored basidia.

Besides the type which is characterized by the gray colour of the lamellae, we found other forms which differ from it in the colour variation of the lamellae from white to cream.

***Tricholoma albobrunneum* (Pers. ex Fr.) Quél.**

(Plate IV figure D)

Fl. Myc. France: 89. 1888.

Under *Pinus halepensis*, growing in groups; immersed in the needle layer, only the upper part of the pileus is visible. In terra rossa soil, Ca: Mt. Carmel, 400 m, 8.12.1951 Z. Samish, 22.12.1951 H; in brown rendzina soil, P: Ben Shemen, 150 m, 14.2.1944 I. Wabl; In gray calcareous soil, EV: Mishmar Haemek, 125 m, 21.1.1945 I. Borovsky; in terra rossa soil, LG: Kefar Hahoreh (near Nazareth), 600 m, 10.1.1945 I. Wabl; J: in terra rossa soil, Jerusalem, 750 m, 10.12.1940 H.

Pileus of our specimens slightly viscous, glabrous, with dark, radiate, innate fibrils; colour "Chestnut Brown" or "Cameo Brown", varies in its intensity, colour of dried herbarium specimens "Bone Brown", "Mars Brown" or "Rood's Brown";

colour of the stipe "Pinkish-Buff", becoming darker and resembling the colour of the pileus, while the upper part remains pale often like a distinct annular zone. Spores $4.5-5.5$ (6) $\mu \times 3.5-5.5$ μ , globose or subglobose, smooth, white in mass; iodine reaction completely negative with Melzer's reagent even if treated after ammonia. Basidia mostly two-spored, sometimes one or three, very seldom four-spored, clavate (18) $22-26$ $\mu \times 4.5-6$ μ ; sterigmata $3-6$ μ long.

Anatomical structure of the cuticle is as follows: Epicutis $50-200$ μ thick, consisting of loose, thin, hyphae ($1.5-2.0$ μ) of pale ochre-brown colour, encrusted with pigmented granules, arranged somewhat irregularly, but most of them more or less parallel to the surface. Subcutis $50-150$ μ thick, consisting of brown, thin ($1-2$ μ) hyphae which are arranged towards the epicutis somewhat irregularly, but below are parallel to the surface. Hypodermium pale with hyphae arranged parallel to the surface, becoming broader ($3-6$ μ) and irregularly arranged towards the cortex. Trama-hyphae $4.5-6$ μ in diameter, those which are close to the hymenium are only $1.5-2.5$ μ ; the subhymenium is very thin. No clamp connection found in any part of the pileus.

Fam. CORTINARIACEAE

Hebeloma longicaudum (Pers.) Quél.

(Plate IV figure E)

Champ. Vosg.: 315. 1872. — *Agaricus longicaudus* Pers. Syn. Meth. Fung.: 332. 1801.

Scattered or in small groups. In sandy brown red soil in open forest of *Quercus ihaburensis* trees. Sh: Even-Yehuda, 40 m, 27.3.1953, 15.2.1954, 4.3.1956 H.

Spores almond-shaped, lemon-shaped, or fusiform, with a hyaline basal apiculus, finely punctate, (10.5) $12-13.5$ $\mu \times 5.25-6$ μ ; yellowish-ochre, ochraceous brown ("Tawny-Olive", "Saccardo's Umber") in mass. Cheilocystidia filamentous, clavate, $4.5-6$ μ wide near the top.

Gymnopilus spectabilis (Fr.) Sing.

(Plate IV figure F)

Agaricales: 561. 1949. — *Pholiota spectabilis* Gill. Champ. Fr.: 443. 1874. — *Agaricus spectabilis* Fr. Elench.: 28. 1828.

In large caespitose groups attached to the base of *Eucalyptus rostrata* trees. Sh: Gan Shmuel, 25 m, 5.1.1941 R₁; Hadera, 40 m, 22.11.1956 H; Givat Haim, 25 m, 15.2.1954 A. Gill; Hadassim, 40 m, 17.1.1954 E. Virsutski; UJ: Shaar-Hagolan, 200 m, below sea-level, 1.1.1954 A. Gishri.

Spores $7.5-9$ $\mu \times 4.5-6$ μ ; verrucose, widely fusiform or almond-shaped; colour in mass "Ochraceous-Orange" to "Ochraceous-Tawny". Basidia $18.5-24$ $\mu \times 5.5-7.5$ μ . Sterigmata $1.5-3$ μ long. Cystidia flask-shaped, $22-26$ $\mu \times 4.5-5.25$ μ , capitate. Ground colour of the pileus "Ochraceous Buff", later orange ochre ("Mars Yellow"), covered with individually distinct, appressed fibrillose squamules and with innate fibrils of rust colour ("Xanthine Orange"); in the centre rust brown ("Sanfords Brown").

Our fungus conforms with the description given by various authors for *Pholiota* (*Gymnopilus*) *spectabilis*. *Ph. spectabilis* comprises, according to Lange (1935–1940), Rea (1922), Maublanc (1946), A. H. Smith (1949) and Singer (1949), several forms from fibrillose to innate squamulose, and perhaps (Lebedeva 1949) granular floccose squamules. Our specimens are innate fibrillose or covered with individually distinct appressed fibrillose squamules. In all the five localities we found our fungus connected exclusively with *Eucalyptus*, while Singer (1949) stated that *Gymnopilus spectabilis* is never associated with *Eucalyptus*.

Another *Gymnopilus* connected with *Eucalyptus* was described in South America and Australia as *G. pampeanus* (Speg.) Sing., but the pileus of our fungus is innately fibrillose, whereas that is not the case for *G. pampeanus* (Singer 1949).

Fam. AMANITACEAE

Amanita vaginata (Bull. ex Fr.) Quél.

(Plate V figure A)

Syst. Myc. 1: 14. 1821. — *Agaricus vaginatus* Bull. Champ. Fr.: t. 98 et 512. 1780–1798. — *Amanitopsis vaginata* Roze in Karsten, Hattsv.: 6. 1879. In a wood of *Quercus ithaburensis* mixed with planted *Pinus halepensis* trees. EV: Tivon (near Nazareth), 170 m, 29.3.1957, 11.4.1957 W.

Colour of the pileus pale cream-gray; often covered with fragments of the *velum universale*. Spores (9.75) 10.5–12 (15) $\mu \times$ (16) 9 (12) μ , subglobose or shortly ellipsoid, nonamyloid, white in mass. Basidia mostly tetrasporic, 30–39 μ long, 11.25–12.75 μ thick; sterigmata 3–5.25 μ long.

Amanita ovoidea (Bull. ex Fr.) Quél.

(Plate V figure B)

Champ. Vosg.: 230. 1872.—*Agaricus ovoidens* Bull. Champ. Fr. 8: t. 364. 1787. In *Pinus halepensis* forest. Terra rossa soil, Ca: Beth Oren, 350m, 20.1.1957 A. Rishpi; Mt. Carmel, 400 m, 31.12.1949 W; Horshat Haarbaim, 28.12.1954 W; gray calcareous rendzina soil, EV: Mishmar Haemek, 125 m, 20.1.1953, 1.12.1953 Rs; gray calcareous rendzina soil, Zeid Wood, 150 m, 15.1.1953 M. Zaharoni. In *Quercus calliprinos* wood, terra rossa soil, J: Jerusalem, 700 m, 13.11.1953 Sh. Hadassi; Aqua-Bella, 700 m, 8.12.1953 P. Emeth; Kiryat Anavim, 700 m, 1.12.1951 G. Rosenberg, 20.12.1952 D. Schleisner.

Spores 9–12 $\mu \times$ 5.25–7.5 μ short cylindrical or ellipsoidal, amyloid, white in mass.

Amanita boudieri Barla

(Plate V figure C)

Bull. Soc. Mycol. Fr. 3: 195. 1887.

Brown-red sandy soil. In a fifteen year old *Eucalyptus rostrata* grove, Sh: Pardess-Hanna, 65 m, 20.1.1941 S. Duvdevani, 3.1.1945 H.

Spores (8.25) 9.5–12 (15.75) $\mu \times$ (4.5) 5.25–6 (7.25) μ . Basidia 33–45 $\mu \times$ 9 (12) μ .

***Amanita vittadinii* Moretti** (Plate V figure D)

Aman. illustr.: 31, t. 1. 1826.

Between dumps, brown-red sandy soil, P: Rehovot, 50 m, 1912. 1956 H; Sh: between dry *Cactus* plants, brown-red sandy soil, Ramoth-Hashavim, 50 m. 20.2.1953 Y. Gertner; under a tree of *Schinus molle*, EV: Balfouria, 16.1.1955 N. Gazit; solitary, between grasses, Beth-Alfa, 75 m, 30.1.1953 A. Sheflan; under *Acacia* trees, alluvial soil, Balfouria 90 m, 21.3.1953 N. Gazit.

As this species is known not to be widely distributed, we are giving here a full description of our specimens.

Pileus 8–24 cm broad, subglobose, then hemispheric, finally convex or convex-plane with a plane disc which is sometimes depressed; margin when young incurved, appendiculate, lacinate with acuminate teeth, striate underneath, surface of pileus including the margin covered with imbricate verrucose-pyramidal-truncate squamules; white or "Pale Pinkish Buff", squamules becoming dirty brown at their margin when old. Lamellae free, ventricose, 12–32 mm wide, whitish or pale yellow-greenish ("Margarite Yellow"), edge white, lamellules obliquely truncate. Stipe 10–17 cm long, 20–50 mm thick, equal, cylindrical or slightly widening downwards and then attenuating towards the base, apex sometimes narrower; white or whitish; covered with imbricated scales arranged more or less in circles, margin of squamules becoming dirty brown when old. Annulus superior, obliquely pendulous, double, on the upper surface glabrous, fibrillose-villose underneath; margin with acuminate teeth. Flesh white or pale yellow-greenish, spongy in the pileus, thick (up to 27 mm), more or less fibrous in the stipe. Spores 9–10.5 (12) $\mu \times$ 6–7.5 (9) μ ; broadly ellipsoid. Basidia 33–40 $\mu \times$ 9–10.5 μ two- and four-spored, rarely one-spored.

Fam. *STROPHARIACEAE****Stropharia coronilla* (Bull. ex. Fr.) Quél.** (Plate V figure E)

Champ. Jura: 255. 1872. — *Agaricus coronillus* Bull. Champ. Fr.: t. 597. 1793.

In grassy fields, growing in large numbers. Terra rossa soil, J: Jerusalem, 750 m, 1.1.1955 M. Aschner; terra rossa soil, UG: Rosh-Pinah, 420 m, 23.12.1955 A. Hadani.

Colour of the pileus "Warm Buff", later ochre ("Yellow Ocher", "Antimony Yellow", "Deep Chrome"), when dry paler; margin whitish. Spores (6.75) 7.5–8 (10.5) $\mu \times$ 3.75–5.25 μ , ovoid, brown-violet ("Walnut Brown", "Army Brown") in mass.

Fam. *SECOTIACEAE****Montagnites candollei* Fr.** (Plate VI figure A)

Epicr.: 241. 1836–1838. — *Agaricus arenarius* DC. Fl. Fr. 6: 45. 1815.—*Montagnea candollei* Fr. ap. Corda, Icon. Fung. 6 (ed. Zobel): 85, pl. 20, f. 146. 1854.

According to the habitats and spore measurements it seems that two types of this fungus have been found until now in Israel :

Type (1)

In sandy soil, P: Rehovot, 50 m, 20.3.1951 *Rt*; CN: south of Beersheba, 6.4.1950 *Rt*.

Spores (4.5) 7.5–10.5 (15) $\mu \times$ 3.75–6 (9.75) μ , fuscous-black in mass, dark brown under the microscope, with a distinct germ pore present; ellipsoid-ovoid, and many of irregular and malformed shape (Figure 4a).

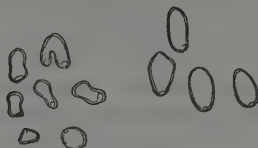


Figure 4

Type (2)

In sandy soil, P: Tel Aviv, 25 m, 8.5.1923 *Rt*; near Gaza, 75 m, 3.5.1924 *Rt*.

Spores (4.5) 12–13.5 (17.25) $\mu \times$ (4.5) 6.75–9 (12) μ ellipsoid ovoid, only few of irregular shape.

The cortex of the pileus of the two types consists of thin 1–2 μ radially arranged crowded hyphae, which are parallel to the surface, colour of hyphae being straw yellow or brownish-yellow.

The genus *Montagnites* has a vast distribution: southern Europe, North Africa, south-western Asia, western part of both Americas, Australia and Galapagos. In all the regions where *Montagnites* occurs it manifests specific ecological characteristics, always according to xerothermic-climatic and edaphic requirements.

The following eight species of *Montagnites* (*Montagnea*) hitherto described are summarized in Table II.

The range of spore sizes in all these species as gathered from Table II varies considerably from 4–6 μ to 15–26 μ in length, and from 3–4 μ to 9–15 μ in width.

Hollos, (1903) after having examined all these collections, came to the conclusion that they all belong to one species, namely, *M. radiosus*. He even assumed that the spore sizes in each of the so-called species collected from various regions and habitats vary and are not permanent; his Hungarian collection showed a majority of elliptical spores of 20 \times 10 μ , but in the same specimen roundish spores of 4–6 μ in diameter were found. Nevertheless he admits that the majority of the spores in each collection reveal uniform sizes.

We are of the opinion that the spore sizes of each collection must be considered as permanent. The occurrence of variations in the range of spore size may be ac-

TABLE II

Species	Place	Spore sizes (μ)	Sources
<i>M. arenarius</i> DC.	North & West America	12—19 \times 6—11.2	Zeller (1943)
" "	Australia	19—24 \times 11—12.8	Morse (1948)
" "	"	15—26 \times 9—15	" "
" "	"	7.5 \times 4.4	" "
<i>M. argentina</i> Speg.	Argentina	14—12 \times 7—10	Hollos (1903)
<i>M. candollei</i> Fries.	France	12 \times 5—6	" "
" "	Algeria	12 \times 5—6	" "
" "	Tunisia	12 \times 5—6	" "
" "	Egypt	12 \times 5—6	" "
" "	Greece	12 \times 5—6	" "
" "	Russia	12 \times 5—6	Zeller (1943)
<i>M. ellioti</i> Mass.	Egypt*	6—7.75 \times 4.5—5	" "
<i>M. haussknechti</i> Rabh.	Caspian Sea	5.7 \times 3—4	Hollos (1903)
" "	Arabia	5.7 \times 3—4	" "
" "	Russia ?	12 \times 4	" "
<i>M. radiosus</i> (Pall.) Holl.	Hungary	12—16 \times 7—10	" "
" "	"	20 \times 10	" "
" "	"	4—6 \times 4—6	" "
" "	Egypt	—	Reichert (1921)
<i>M. tennis</i> Pat.	North Africa	7—8 \times 4—5	Hollos (1903)
" "	Galapagos	5—6.5 \times 4—4.5	Zeller (1943)

counted for by teratological malformations as shown by Heim (1932) in the genus *Podaxon*.

Perusing all the figures obtained of spore measurements from various countries and collections, one may discern three types of collections showing various spore sizes, which seem to differ from each other significantly:

- (1) The small-sized spores — 5–8 μ long and 4–5 μ broad.
- (2) The medium-sized spores — 12–16 μ long and 5–7 μ broad.
- (3) The large-sized spores — 20–26 μ long and 9–15 μ broad.

On the basis of measurement of 100 spores from each of the five localities of *Montagnites* in Israel, it seems that only two types do occur here, type (1) and type (2). These two types found in Israel resemble each other macroscopically, differing only in the thickness of the stipe, type (1) being more slender than type (2). They seem to differ in their ecological habitats, as type (1) was found in drier places: south of Beersheba and Rehovot, whereas type (2) was found near the sea-shore in Tel Aviv and Gaza.

The marked variation of the sizes and shapes of the spores even in the same specimen noticed by Hollos (1903) was found also in our material and specially

* Not New Zealand as stated by Saccardo, and sizes of spores not 12 \times 7 μ as described by him.

pronounced in type (1). In addition to the size variation a malformation of spores was observed. This irregularity of shape reaches approximately 50 per cent.

One would be tempted, to consider the three types mentioned above as separate species, but in the absence of comparative material from other countries we would rather refrain now from such a conclusion.

Fam. SCLERODERMATACEAE

Pisolithus tinctorius (Mich. ex Pers.) Coker et Couch. (Plate VI figure B)

Gasteromycetes of the Eastern United States and Canada: 170. 1928. — *Scleroderma tinctorium* (Mich.) Pers. Syn. Meth. Fung.: 152. 1801.

Common under *Eucalyptus* trees. Under 2–3-year-old tree, Sh: Emek-Hefer, Midrashat-Ruppin, 18.10.1953 H; in sandy soil, P: Rehovot, 50 m, 10.12.1950 I. Kaplan, 20.10.1954 H, 15.10.1952, 29.10.1953 Rt; EV: Beth Alfa, 60 m, 12.12.1950 H.

Spores globose (6) 7.5–9 (12) μ , echinulate, spine-length 1–2 μ .

We found this fungus always associated with *Eucalyptus* trees. The same was found by Bottomley (1948) in South Africa and that confirms once more the close relationship between these trees and *Pisolithus tinctorius*. This relationship is considered as a symbiosis by van der Byl (Ref. Bottomley 1948).

Fam. LYCOPERDACEAE

Disciseda cervina (Berk.) Hollos (Plate VI figure C)

Novenyntani Koslem: 107. 1902. — *Bovista cervina* Berk. Ann. Nat. Hist. 9: 447. 1842.

This fungus was found in large numbers in brown red sandy soil of uncultivated land. P: Rehovot, 50 m, 14.11.1957 and 25.12.1957 H.

Gleba in the mature powdery stage "Olive-Brown". Spores 6.75–7.5 (9) μ globose, verrucose. Capillitium threads 2.25–5.25 μ in diameter.

Myriostoma coliforme (Dicks.) Corda (Plate VI figure D)

Anleitung z. Studium d. Mycologie: tab. D. 1842. — *Lycoperdon coliforme* Dicks. Plant. Crypt. Brit. 1: 24. 1785.

In sandy soil under *Acacia farnesiana* trees. P: Rehovot, 50 m, 2.12.1954 and 1.1.1955 R. Kenneth.

Spores 5.25–6.75 μ , brown ("Saccardo's Umber"), echinulate, covered with a hyaline episporium. Capillitium pale brown, 2.25–3.75 μ in diameter, thick-walled, tapering at the ends, non-branched.

Fam. TULOSTOMATACEAE

Battarea guicciardiniana Ces. (Plate VI figure E)

Atti d. R. Accad. Sci. Vol. 7. 1875.

Ca: Zikhron-Yaacov, 300 m, 1.6.1940 *A. Gerinker*; under *Lantana* bushes, P: Ben Shemen, 100 m, 23.6.1940 *I. Wabl*; in brown red sandy soil, under *Duranta* sp. bushes; Rehovot, 50 m, 22.11.1951 *H*; 15.11.1952 *I*; 28.2.1955 *R. Shilo*; in a ploughed field, Naan, 8.2.1948 *H*; EV: Ein Harod, 0–50 m, December 1926 *N. Naftolsky*; Beth-Alfa, 75 m, 23.11.1951 *A. Sheflan*; Basaltic soil, *Beth-Hashita*, 0–50 m, 1.11.1953 *B. Sabo*; alluvial soil, UJ: Beth-Zerah, 100 m, below sea-level, 2.8.1934 *Rt*.

Gleba brown ochre ("Hazel", "Argus Brown"). Spores 5.25–6.75 μ , roundish verruculose, under the microscope yellowish-ochraceous. Elaters: 5.25–7.5 μ wide. Capillitium threads (4.5) 5.25–6 (7.5) μ thick.

Numerous species were described in the genus *Battarea* Pers. by various authors. They were all reduced by Hollos (1903) to one variable species, *Battarea phalloides* (Dicks.) Pers. Lloyd (according to Fisher 1933) left two species: *B. phalloides* (Dicks.) Pers. and *B. digueti* Pat., the last being well characterized by its apical dehiscence. Other authors like Fisher (1933), Petri (1909) and Alexandri (1934) recognized two species, *B. phalloides* and *B. stevenii* (Libosh) Fr. or *B. guicciardiniana* Ces. which differ by the following main features:

B. phalloides is characterized by (1) a slender habit; (2) a simple volva, (3) gelatinous volva in the egg stage; (4) a membranous volva when dry; (5) finely punctated spores. *Battarea guicciardiniana* is characterized by its (1) robust habit; (2) thick and double volva; (3) large and verruculose spores.

Rea (1942) is of the opinion that the difference in habit between the species should not be considered as typical and permanent because he found intergrading specimens in his collection of California. It seems that Rea did not take into account the ornamentation of the spores. Petri (1909) and Alexandri (1934) examined the original material found by Cesati and they both confirmed that the spores of *B. guicciardiniana* (*B. stevenii*) are verruculose, while those of *B. phalloides* are almost smooth, only very slightly punctate. The spores in our specimen show a pronounced verruculose structure, thus distinguishing it clearly from the spores of *B. phalloides*. The double volva found in our material is a second proof that we have here a quite different species from *B. phalloides* which is described as possessing a simple volva.

Fam. NIDULARIACEAE

Cyathus olla Pers.

(Plate VI figure F)

Syn. Meth. Fung.: 237. 1801.

On twigs under an *Acacia* sp. tree. P: Rehovot, 2.11.1957 *E. Dromi*.

Spores (6) 7.5 (9) $\mu \times$ 6–6.75 (7.5) μ , ovoid, broadly elliptical, subglobose. The spores of our fungus seem smaller than those described by Rea (1922), but their dimensions agree with those given by Cunningham for New Zealand (1924), Bottomley for South Africa (1948) and Coker and Couch (1928) for *C. vernicosus* (= *C. olla*) in North America.

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The species *Amanita boudieri* was determined with the help of the late Mr. E. J. Gilbert.

The species *Tricholoma albobrunneum* was determined with the help of Prof. A. H. Smith of the University of Michigan and we are happy to have the opportunity to thank him for his kindness.

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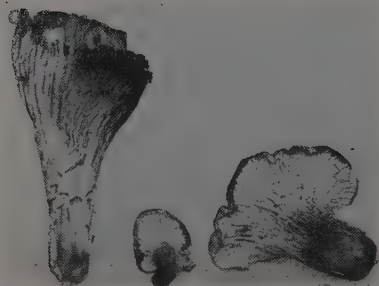
PLATE I



A



B



C



D



E



F

A. *Caloporus leucomelas*, B. *Clavulina cinerea*, C. *Cantharellus cibarius*, D. *Xerocomus chrysenteron*, E. *Boletus aveluti* var. *lateritius*, F. *Paxillus panuoides*.

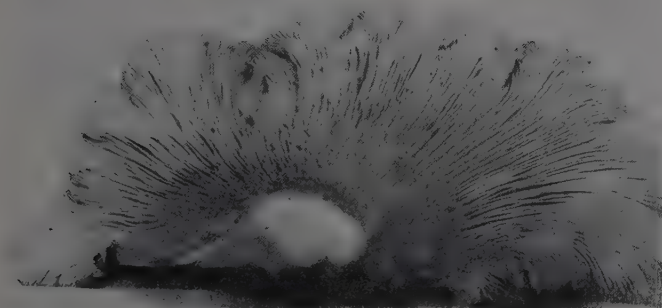
PLATE II



B

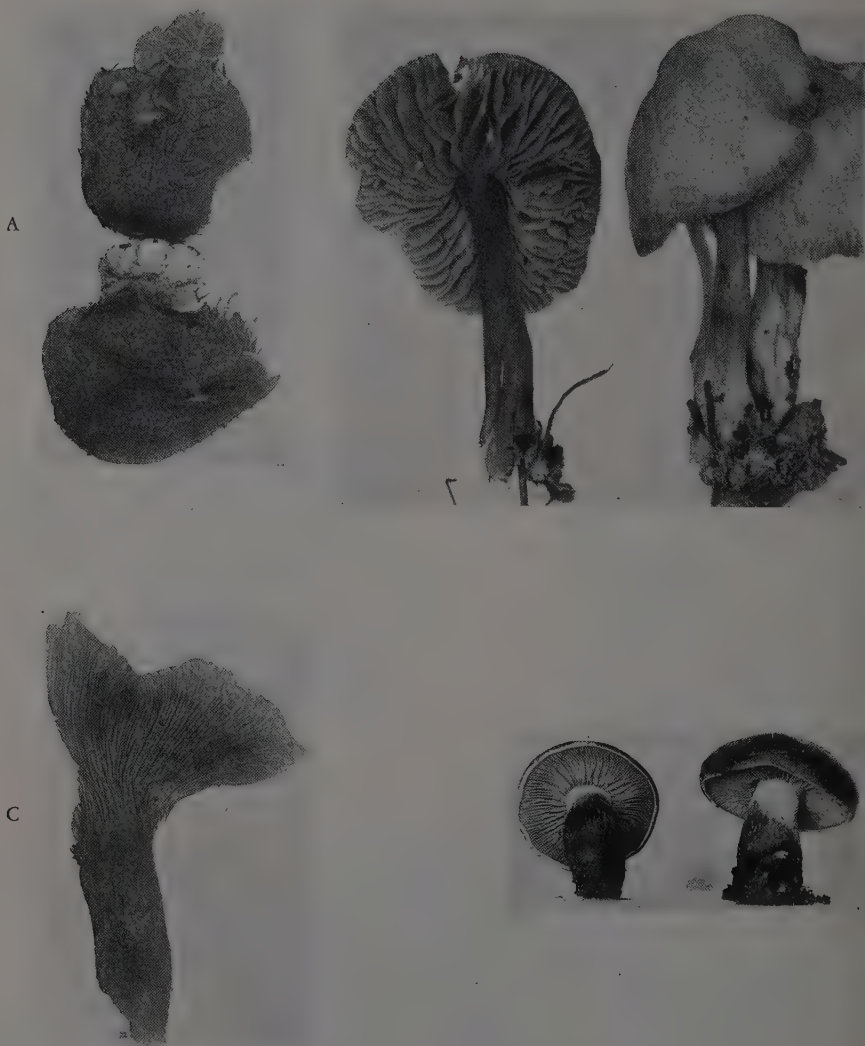


D



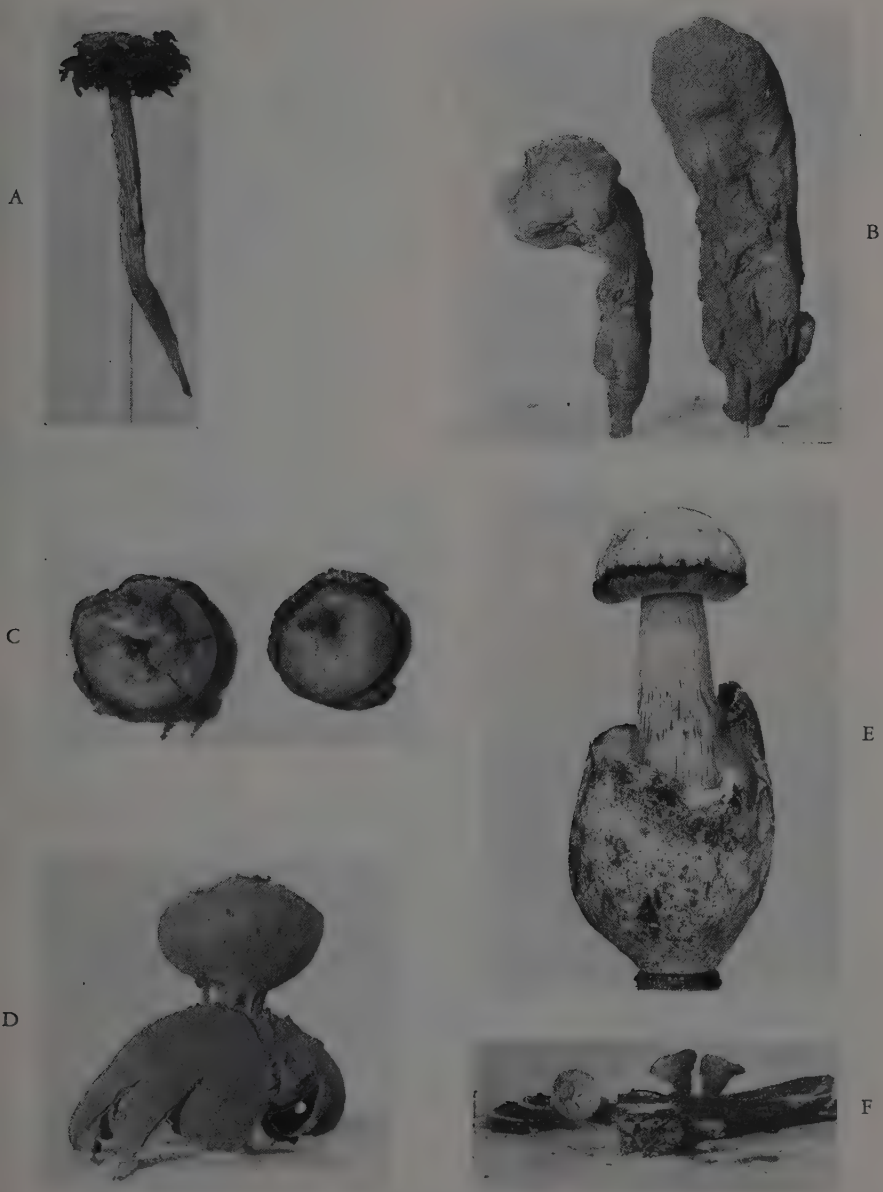
A. *Gomphidius viscidus*, B. *Lactarius deliciosus*, C. *Russula alutacea*, D. *Pleurotus eryngii*, E. *Pl. salignus*.

PLATE III



A. *Crepidotus variabilis* var. *stercorarius* var. nov., B. *Mycena pura*, C. *Omphalotus olearius*, D. *Lepista nuda*.

PLATE IV



A. *Lepista sordida*, B. *L. sordida* var. *gracilis* var. nov., C. *Tricholoma weizianum* sp. nov., D. *Tricholoma albobrunneum*, E. *Hebeloma longicaudum*, F. *Gymnopilus spectabilis*.

PLATE V

A



B



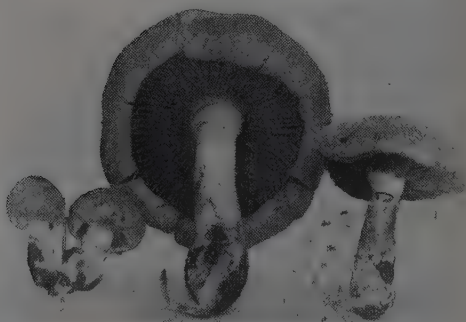
D



C

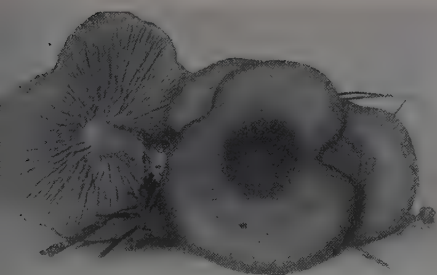


E

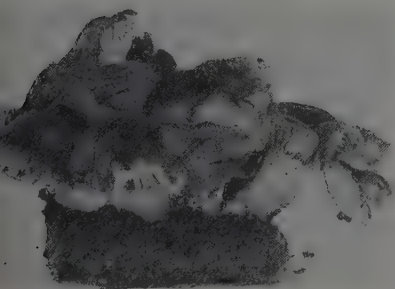


A. *Amanita vaginata*, B. *A. ovoidea*, C. *A. bondieri*, D. *A. vittadini*, E. *Stropharia coronilla*.

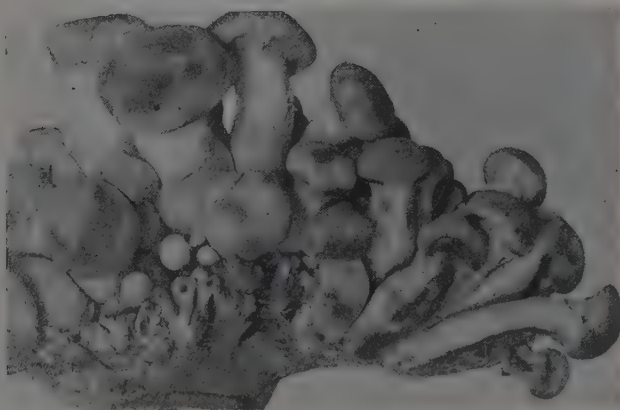
PLATE VI



B



D



F

A. *Montagnites candollei*, B. *Pisolithus tinctorius*, C. *Disciseda cervina*, D. *Myriostoma coliforme*, E. *Battarea guicciardiniana*, F. *Cyathus olla*.

SEEDLING HETEROPHYLLY IN THE CALIFORNIA FLORA

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ABSTRACT

In a large number of native californian species belonging to various families, the seedlings and juvenile stages bear leaves less lobed, dissected, or compound than those of mature shoots. In a smaller number of species the juvenile leaves are lobed or compound and those of adult shoots are simple. Many species with simple juvenile and lobed or compound adult leaves, particularly those which form shrubs or trees, occur in mesophytic habitats. Those with reduced leaves on the mature shoots consist chiefly of shrubs inhabiting regions with the Mediterranean type of climate characterized by cool, moist winters and hot, dry summers. The significance of these facts is discussed in relation to phylogenetic, ecological, and morphogenetic explanations of heterophylly.

Botanists are well aware of the fact that the seedlings and young shoots of many species of plants bear leaves which are entirely different in shape from those on the adult shoots. This phenomenon has been well described by Massart (1894), and discussed by such morphologists as Goebel (1928), Takhtajian (1954), and others. Nevertheless, new information has recently been acquired from the fields of ecology and morphogenesis which bears upon the problem of the origin of heterophylly, and genetic material has recently been made available by means of which heterophylly can be made to serve as a particularly useful medium for learning more about the relationship between gene action and morphological differences in plants. Hence further discussion of this phenomenon seems appropriate at this time. I also consider appropriate the inclusion of this article in a volume dedicated to Professor Michael Zohary, whose botanical career has been so brilliantly devoted to clarifying the origin and evolution of the flora of his native land on the basis of every possible type of evidence. In the scope of a brief article such as this, however, I must confine my attention to the native flora of a particular region, California, which I know best, and to terrestrial dicotyledonous angiosperms among plants.

In the strictest sense of the word, all plants can be said to possess heterophylly, since the juvenile leaves are always smaller and possess different patterns of venation from those of the mature shoots. The present discussion will, however, be confined to examples in which the juvenile and adult leaves differ strikingly from

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each other in form. The California species of dicotyledons with this property fall into two types: those in which the juvenile leaves are simpler in form than the adult leaves, and those in which they are more complex. In the present account, these are termed respectively the elaboration and the reduction type. Two additional types, represented by *Acacia*, in which the adult shoots bear phyllodes rather than leaves; and *Eucalyptus*, in which the adult leaves differ chiefly in shape and position; are well known among the cultivated plants of California, but are not found in the native flora.

Table I lists the principal California species with each of the two types of heterophylly, and gives some data on their distribution and habitat. In order to keep the table within reasonable limits, the numerous examples in the Legumi-

TABLE I

Principal species of California dicotyledons with seedling heterophylly.

A. Species with elaboration heterophylly; seedling leaves more simple, adult leaves more complex or compound

Family	Genus and Species		Principal life form* and Habitat
Fagaceae	<i>Quercus lobata</i>	T	Lowland valleys, deep soil
Fagaceae	<i>Quercus garryana</i>	T,S	Mesic forests, montane valleys
Fagaceae	<i>Quercus kelloggii</i>	T	Mesic forests
Juglandaceae	<i>Juglans</i> spp.	T	Forests, valleys in deep soil
Polygonaceae	<i>Rumex</i> spp.	P	Moist meadows
Portulacaceae	<i>Montia perfoliata</i>	A	Shade of trees or shrubs
Ranunculaceae	<i>Delphinium</i> spp.	P	Various
Ranunculaceae	<i>Ranunculus</i> spp.	P	Moist or seasonally moist meadows
Berberidaceae	<i>Berberis (Mahonia)</i> spp.	S	Various
Papaveraceae	<i>Romneya coulteri</i>	P	Stream beds and canyon bottoms
Cruciferae	<i>Stanleya pinnata</i>	P	Deserts
Cruciferae	<i>Thelypodium</i> spp.	A	Deserts and dry hillsides
Cruciferae	<i>Barbarea vulgaris</i>	P	Stream banks
Cruciferae	<i>Radicula</i> spp.	P	Moist places
Cruciferae	<i>Dentaria</i> spp.	P	Mesic forests
Platanaceae	<i>Platanus racemosa</i>	T	Stream banks
Rosaceae	<i>Lyonothamnus floribundus</i>	T,S	Chaparral
Rosaceae	<i>Rubus</i> spp.	S	Forests, stream banks
Rosaceae	<i>Fragaria</i> spp.	P	Forests
Rosaceae	<i>Potentilla</i> spp.	P	Forests, meadows, mountain slopes
Rosaceae	<i>Geum</i> spp.	P	Forests, mountain slopes
Rosaceae	<i>Rosa</i> spp.	S	Forests, stream banks
Rosaceae	<i>Sorbus sitchensis</i>	S	Montane forests
Leguminosae	Various genera and spp.	T,S, P,A,	Various
Anacardiaceae	<i>Rhus diversiloba</i>	S	Forests, brushy places

* T — tree, S — shrub, P — perennial herb, A — annual herb.

TABLE I (continued)

Family	Genus and Species		Principal life form and Habitat
Aceraceae	<i>Acer</i> spp.	T	Forests, stream banks
Malvaceae	<i>Sidalcea</i> spp.	P	Meadows
Loasaceae	<i>Mentzelia lindleyi</i>	A	Dry slopes, in chaparral
Onagraceae	<i>Oenothera scapoidea</i>	A	Deserts
Onagraceae	<i>Oenothera brevipes</i>	A	Deserts
Araliaceae	<i>Aralia californica</i>	P	Stream banks
Umbelliferae	Various genera and spp.	P,A	Various
Oleaceae	<i>Fraxinus</i> spp.	T,S	Forests, stream banks
Polemoniaceae	<i>Polemonium</i> spp.	P	Moist or dry slopes, montane
Polemoniaceae	<i>Gilia</i> spp.	P,A	Various
Hydrophyllaceae	Various genera and spp.	P,A	Various
Labiatae	<i>Salvia columbariae</i>	A	Dry slopes
Scrophulariaceae	<i>Tonella tenella</i>	A	Wooded slopes
Scrophulariaceae	<i>Castilleja</i> spp.	P	Meadows, montane slopes
Scrophulariaceae	<i>Orthocarpus</i> spp.	A	Meadows
Scrophulariaceae	<i>Cordylanthus</i> spp.	A	Dry slopes
Scrophulariaceae	<i>Pedicularis</i> spp.	P	Meadows, forests
Caprifoliaceae	<i>Sambucus</i> spp.	S	Forests, stream banks
Compositae	Various genera and spp.	S,P,A	Various

B. Species with reduction heterophylly; seedling leaves more complex or compound, adult leaves more simple

Family	Genus and Species		Principal life form and Habitat
Fagaceae	<i>Quercus douglasii</i>	T	Dry slopes
Fagaceae	<i>Quercus chrysolepis</i>	T,S	Dry slopes
Papaveraceae	<i>Dendromecon rigidum</i>	S	Dry slopes
Rosaceae	<i>Adenostoma fasciculatum</i>	S	Dry slopes
Rhamnaceae	<i>Ceanothus cuneatus</i>	S	Dry slopes
Ericaceae	<i>Arbutus menziesii</i>	T	Dry forests
Ericaceae	<i>Arctostaphylos</i> spp.	S	Dry slopes
Hydrophyllaceae	<i>Eriodictyon</i> spp.	S	Dry slopes
Scrophulariaceae	<i>Collinsia heterophylla</i>	A	Dry, shady slopes

nosae, Umbelliferae, Hydrophyllaceae, and Compositae have not been listed separately. From a survey of this table, the following facts are evident. In the first place, the examples of both types are scattered through the dicotyledons without any definite plan, although the elaboration type is particularly common in the four families mentioned above. Second, the elaboration type is by far the most common, and is found in trees, shrubs, and herbs approximately in proportion to the frequency of these growth forms in the flora. The reduction type, with a single exception, *Collinsia heterophylla*, is confined to shrubs or to small trees which have shrubs among their close relatives. Third, the habitat distributions of the various types are by no means at random. The elaboration type is found chiefly in mesophytes, and nearly all of the woody plants in this group are mesophytic. Among the annuals there are a number of species found in xeric or even desert habitats

(*Thelypodium* spp., *Mentzelia lindleyi*, *Oenothera* subg. *Chylismia*, various Leguminosae, Hydrophyllaceae, and Compositae), but these may be largely mesic in their moisture tolerance, since many desert annuals grow only during the wetter season. The coarse perennial species, *Stanleya pinnata*, along with various species of Leguminosae (esp. *Astragalus*) and Compositae (*Franseria*, *Bahia*, *Chaenactis*, *Achillea*, *Senecio douglasii*) are exceptional in being perennials or even shrubs with decidedly xeric preferences associated with the elaboration type of heterophylly.

The few species with the reduction type of heterophylly are confined to a single climatic zone, the Mediterranean, characterized by moist, mild winters and hot, dry summers. The great majority of the species are, furthermore, shrubs belonging to the broad sclerophyll or chaparral formation, which is most characteristic of this zone. The most striking example is *Adenostoma fasciculatum*, or chamise, the commonest and most widespread single species of the California chaparral (Figure 1). In this species, the adult leaves are entire, linear, and needle like, while the juvenile leaves are much thinner, and are ternately compound into fine, linear lobes. A noteworthy fact is that the two species which vie with *A. fasciculatum* for the greatest overall frequency in the California chaparral, *Ceanothus cuneatus* and *Arctostaphylos glandulosa*, also exhibit the reduction type of heterophylly, although to a lesser degree. When we add to this group the numerous other chaparral species of *Arctostaphylos* and the widespread and fairly common *Dendromecon rigidum*, and *Eriodictyon californicum*, we realize that reduction heterophylly is a characteristic feature of the shrubs which compose the California chaparral. On the other hand, it is not found at all to my knowledge, in the shrubs of the desert and cold steppe communities, even though some of these (*Purshia tridentata*) are reasonably closely related to chaparral species (*Adenostoma fasciculatum*). An even more remarkable fact is that the commonest shrubs of the Mediterranean maquis, the Old World counterpart of chaparral, do not exhibit this phenomenon. It is completely lacking in such genera as *Cistus*, *Olea*, *Phillyrea*, and *Calycotome*. A type of reduction heterophylly occurs in some Mediterranean genera of the Leguminosae, tribe Genisteae, such as *Cytisus*, *Spartium*, *Ulex*, and *Erinacea*, in which the juvenile stages possess well developed leaves but the adult plants are essentially leafless. One of the commonest shrubs of the maquis, *Pistacia lentiscus*, is remarkable for this habitat in having elaboration heterophylly. The writer has not seen seedlings of *Arbutus andrachne*, but it presumably has the same type of reduction heterophylly as its relative in California, *A. menziesii*.

Three types of explanations have been offered for seedling heterophylly; phylogenetic, ecological, and morphogenetic. These explanations are complementary to each other, and neither of them is complete in itself. The phylogenetic explanation is based either on the hypothesis of recapitulation, which maintains that the juvenile leaves of heterophyllous species resemble the adult foliage of some ancestral type; or on that of embryonic or juvenile similarity, which maintains that the juve-

nile leaves of heterophyllous types are similar to those of non-heterophyllous ancestral species, but that the adult leaves of the two types have evolved in opposite directions. For various reasons (Stebbins 1950, chap. 13), the latter hypothesis is believed to have more general validity.

The insufficiency of the phylogenetic explanation becomes evident from the fact that among related genera of the same family some have seedling heterophylly and others do not. On the phylogenetic basis, the remarkable example in *Adenostoma* would be explained by the fact that in many genera of Rosaceae the adult leaves are ternately decompound, and *Adenostoma* probably evolved from such a genus. But there are two other species of Rosaceous shrubs in western North America, *Cowania stansburiana* and *Purshia tridentata*, which, like *Adenostoma*, have much reduced adult leaves, and these are, furthermore, lobed. They also look as if they had been derived from ancestors with compound leaves, and in fact one of their relatives, *Fallugia paradoxa*, has adult leaves much like the juvenile leaves of *Adenostoma*. Yet in *Cowania* and *Purshia* the juvenile leaves are as simple as the adult ones, or even more so. This suggests that reduction of the adult leaves can occur in the Rosaceae without the appearance of reduction heterophylly, and raises the question of why it should be evident in some groups and not in others.

A similar but even more perplexing example is that of *Collinsia heterophylla*. The difference between the elaborately compound juvenile leaves of this species and the simple, oblong leaves of the adult stems is as striking as the heterophylly in *Adenostoma*. Yet in most of the other species of *Collinsia*, as well as in the great majority of the genera in the tribe Cheloneae of the Scrophulariaceae, both juvenile and adult leaves are entire. *Tonella*, a monotypic genus closely related to *Collinsia*, has the elaboration type of heterophylly, and the same condition may exist in certain Old World species of *Scrophularia*, in which the adult leaves are lobed or divided. But morphological evidence indicates that the derivation of *C. heterophylla* from *Tonella* or *Scrophularia* is much less probable than its origin from other species of *Collinsia*. Hence this genus appears to have evolved from a condition in which all of the leaves are simple toward one with compound juvenile and simple adult leaves. This is exactly the opposite of what would be expected on the hypothesis of either recapitulation or embryonic similarity.

The ecological or adaptive explanations of heterophylly can be stated as follows. Elaboration heterophylly is associated with adaptation to habitats in which compound or lobed leaves are at a selective advantage in conjunction with other structural characteristics possessed by the plant. These are usually mesic situations, but some xeric habitats, particularly those subject to violent fluctuations in the amount of available water, may also favour the evolution of compound leaves. Such leaves, however, may have a higher adaptive value on the robust adult shoots than on the more delicate seedlings. Hence mutations for compound leaves have the highest selective value if they act relatively late in development.

Reduction heterophyly, according to the ecological explanation, can be associated with adaptation of mesophytes to more xeric habitats, with an accompanying reduction of the leaf surface. If the xeric conditions prevail throughout the developmental cycle of the plant, selection will favour mutations which act early in development, and produce an equal amount of reduction in both juvenile and adult leaves. If, however, the group is becoming adapted to a climate in which moist, cool conditions prevail during that time when seedlings are developing, while the older plants must survive prolonged periods of extreme drought and heat, then selection can be expected to favour mutations which act late in development and reduce only the adult leaves. This explanation agrees with the fact that reduction heterophyly is prevalent in the coastal regions of California, in which seedling development of the shrub species occurs during the cool winter, when abundant soil moisture is present much of the time, while the adult shrubs must survive several months of complete drought associated with high temperatures and low humidity. In the desert and steppe regions, however, the shrubs undergo at least part of their seedling development in the late spring and summer, when the climate is already hot and dry.

This explanation cannot, however, account for the relative infrequency of reduction heterophyly in the Mediterranean region, which has a climate similar to that of coastal California. If, however, the phylogenetic and ecological explanations are combined, a satisfactory explanation may be forthcoming. The shrubs of the California chaparral belong mostly to families (Rosaceae, Ericaceae, Hydrophyllaceae, Papaveraceae) in which compound, lobed, or at least serrate margined leaves are the commonest type, and in which the leaves are usually thin in texture. The commonest Mediterranean shrubs, on the other hand, belong to families (Cistaceae, Oleaceae), in which entire, thick leaves predominate both in the family itself and in its nearest relatives. *Pistacia*, which belongs to a family with predominantly compound leaves, has somehow adapted itself to the Mediterranean climate without reduction in leaf form. One can postulate, therefore, that because of the genetic nature and past evolutionary history of the shrubby groups which were best adapted to occupying the Mediterranean regions when their characteristic climate first developed, mutations producing leaf reduction late in development did not have the high selective value in them that they did in the groups ancestral to the shrubs of the California chaparral.

Even this combination of explanations is insufficient to account for the anomalous example of *Collinsia heterophylla*. This species lives in shady canyons of the Mediterranean climatic zone, in association with other annual species which have leaves either entire (*Clarkia*, *Plectritis*), lobed or compound (*Nemophila*) throughout their vegetative developmental history. Furthermore, similar habitats in the same climatic zone are occupied by the related species *C. heterophylla*, *Tonella tenella*, and *C. sparsiflora*, the first of which has reduction heterophyly, the second

elaboration heterophylly, and the third possesses entire leaves throughout. This group of species surely offers a challenging problem in evolution.

The morphogenetic explanation of heterophylly is complementary to rather than competitive with the phylogenetic and ecological explanation, since it deals with the mechanisms which govern the development of one or another type of leaf form, rather than the way in which these mechanisms and the resulting forms have evolved and become established. In ferns, which have highly developed sequences of elaboration heterophylly, Wetmore (1954 and unpubl.) has shown that both sporelings and excised apical meristems from adult plants, when grown on artificial culture media, will produce only leaves of the juvenile type if kept in a medium low in sucrose, but will quickly change to the adult type of leaf if the sucrose content of the medium is raised to an abnormally high level. Although generalizations about all plants based only on these results with one group would be dangerous to make, nevertheless a good working hypothesis for future experimentation is that in plants with the elaboration type of heterophylly the juvenile leaf form is favoured by a low rate of carbohydrate metabolism, and the adult form by a high rate. To explain reduction heterophylly on this basis, two hypotheses are possible. One is that in these types, as in ferns, more elaborately compound leaves are favoured by a high rate of carbohydrate metabolism, but that contrary to ferns this rate is relatively high in seedlings and lower in adult plants. The alternative is that these plants, like ferns, progress during seedling development from a low to a higher rate of carbohydrate metabolism, but that the genetic constitution and normal course of development of their leaf primordia is such that these react to changes in level of carbohydrate metabolism in exactly the opposite way from ferns, as well as from dicotyledons with the elaboration type of heterophylly. In favourable material, such as the related annual genera *Collinsia* and *Tonella*, these hypotheses could be put to the experimental test. A solution of this problem might open the door to avenues of approach toward an even more basic problem, that of the way in which genetic differences bring about differences in form. Hence seedling heterophylly, though a rather specialized phenomenon, may serve as a medium for giving us a better understanding of some basic problems of plant biology.

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Figure 1

Top, seedlings of *Adenostoma fasciculatum* (Rosaceae) of three ages, to show juvenile and adult foliage. Bottom, a sequence of individual leaves from these seedlings.

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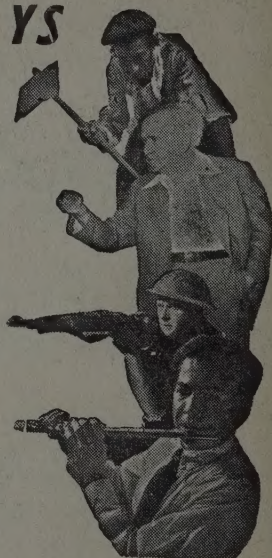
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